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Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence

Marcus Clauss[1,*] & Gertrud E. Rössner[2,3,4]

[1)] *Clinic of Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland (*corresponding author's e-mail: mclauss@vetclinics.uzh.ch)*
[2)] *SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, D-80339 Munich, Germany*
[3)] *Department für Geo- und Umweltwissenschaften, Ludwig-Maximilians-Universität München, Richard-Wagner-Strasse 10, D-80333 München, Germany*
[4)] *GeoBio-Center LMU, Richard-Wagner-Strasse 10, D-80333 München, Germany*

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The omasum of pecoran ruminants (which is absent in tragulids) and shorter gestation periods in non-giraffid crown pecorans (as opposed to giraffids) could represent cases of key innovations that caused disparity in species diversity in extant ruminants. Literature suggests that the different ruminant groups inhabited similar niche spectra at different times, supporting the 'increased fitness' interpretation where a key innovation does not mainly open new niches, but allows more efficient use of existing ones. In this respect, we explored data on fossil species diversity of Afro-Eurasian ruminants from the Neogene and Quaternary. Tragulid and giraffid diversity first increased during the Early/Middle Miocene with subsequent declines, whereas bovid and cervid diversity increased distinctively. Our resulting narrative, combining digestive physiology, life history and the fossil record, thus provides an explanation for the sequence of diversity patterns in Old-World ruminants.

Introduction

Evolutionary progress and key innovations

That progress occurred during evolutionary history at a macroevolutionary level is usually not an issue of debate (e.g. Rosenzweig & McCord 1991). From the anatomy of the first multicellular organisms to complex plants and animals, from the structure of the first terrestrial tetrapod's limb to the unguligrade extremity of larger herbivores (Shubin *et al*. 2006, O'Leary *et al*. 2013), from the addition of the hypocone to the molar morphology of therian mammals (Hunter & Jernvall 1995) — the concept of progress in functional morphology appears intuitive. What is often debated is progress at a microevolutionary level: why does a certain taxonomic group appear to be more successful in terms of speciation than another, like certain spider clades (Bond & Opell 1998) or a certain clade among phyllostomid bats (Dumont *et al.* 2012)? Can we explain this in terms of evolutionary progress and a hypothetical, more efficient functionality, maybe even linked to a certain (and potentially new) niche, in the sense of 'directional evolution' (Liem 1990), or do we choose to consider morphophysiological variety at low taxonomic levels as random variety solving the same problems in different ways (of similar efficiency) in the sense of neutral evolution (ibid.)?

The concept of key innovation plays an important role in the more general concept of evolutionary progress; key innovations may explain competitive displacement (Nitecki 1990, Rosenzweig & McCord 1991, Heard & Hauser 1995, Hunter 1998). Morphophysiological, behavioural and life history peculiarities of a certain clade do not only help to define that clade taxonomically, but represent potential candidates for innovations that helped shape that clade's evolutionary success. However, apart from rare exceptions when fossils also reveal details, e.g. of copulation (Joyce *et al.* 2012), pregnancy, precociality and birth (Gingerich *et al.* 2009), or sociality (Bibi *et al.* 2012), mostly only a certain subset of morphological attributes fossilizes. The emphasis in the concept of key innovations has therefore traditionally been on hard tissue morphological aspects (Burggren & Bemis 1990).

One perceived problem with the concept of key innovation is the tautology amounting from the likewise usage of morphological characters to identify a (diverse) clade and as a reason for its success (diversity). The recent development of deriving phylogenetic estimates from genetic information alleviates this problem and facilitates statistical approaches to test for the effect of certain morphological characteristics on diversification rates in extant species clusters (e.g. Dumont *et al.* 2012). For most fossil taxa, however, the lack of genetic material means that the problem is not readily alleviated. Another solution is to use a character considered to be apomorphic or convergent in several different taxa, which can be compared to closely related taxa in which it is absent (e.g. Hunter & Jernvall 1995). Thus, studies of key innovations in the fossil record often represent narratives, in which the plausibility of the argument is the major indicator of its quality, but the underlying hypothesis cannot be tested statistically.

Hence, phenotypic traits without a potential to fossilize such as soft tissue anatomy, physiology and life history characteristics provide ideal bases to explore key innovations, because they are usually not used to reconstruct phylogenetic relationships. Under the assumption that those traits observed in extant species are representative for the entire clade including fossil species, the adaptive value of such features can be assessed in comparative and even experimental studies on extant species. A prominent example where soft tissue anatomy and physiology was used to explain the evolutionary diversification is the digestive physiology of ungulate herbivores. Using the concept of a difference in the digestive function of hindgut and foregut fermenters (Janis 1976, Duncan *et al.* 1990), Janis *et al.* (1994) have explained the apparent displacement of equids by ruminants, concluding a primarily digestion-driven evolutionary advantage for ruminants. Similarly, the difference in species diversity between Tylopoda and Ruminantia was speculated to result from the differences in functionality of the sorting mechanism that prevents Tylopoda from achieving the higher food intakes observed in many Ruminantia (Clauss *et al.* 2010a). This latter hypothesis correlates well with the apparent replacement of camelids by ruminants in Janis *et al.* (1994). Because of their prominence in specimen and species number in the fossil record, and detailed knowledge about their comparative anatomy and physiology (Clauss *et al.* 2008), ungulate herbivores appear as promising test cases for the exploration of evolutionary success and related key innovations.

Tragulidae, Pecora, and ruminant stomach anatomy

Compelling evidence of extended comparative analyses including phenotypic as well as molecular data (Janis & Scott 1987, Gentry & Hooker 1988, Hernández-Fernández & Vrba 2005, Hassanin *et al.* 2012) supports the view that Tragulidae are the sister group of Pecora, and the most

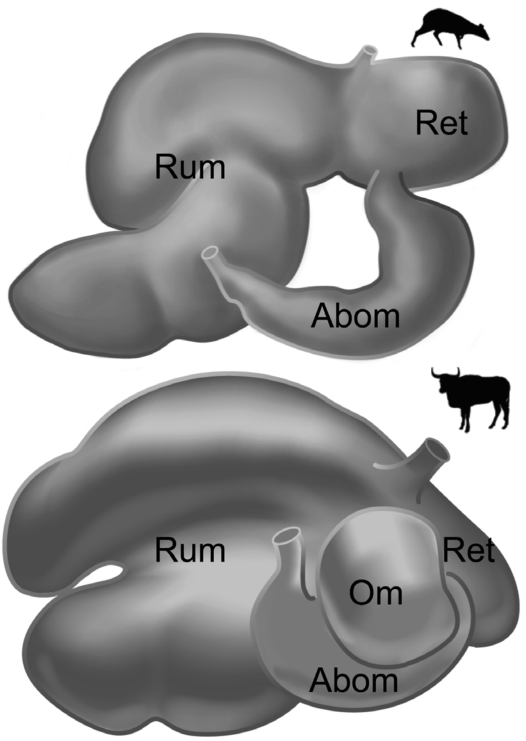

Fig. 1. Schematic representation of the stomach of tragulids (top) and Pecora (bottom). Rum = rumen, Ret = reticulum, Om = omasum (lacking in tragulids), Abom = abomasum. Drawing by Jeanne Peter, after Schmidt (1911) and Hofmann (1969).

basal living ruminant group. The branch-off of the tragulid clade from the ruminant stem lineage is biostratigraphically/biochronologically dated for the Late Eocene in southeast Asia (Métais *et al*. 2001). Molecular clock analyses produced contradicting estimates for the Late Eocene (Hernández-Fernández & Vrba 2005) or Late Oligocene to Early Miocene (Hassanin *et al*. 2012). The pecoran branch-off has been estimated via molecular clock analyses at 33.2 to 27.6 million years ago (mya) (Early Oligocene to Late Oligocene) (Hernández-Fernández & Vrba 2005, Hassanin *et al*. 2012).

The ten currently differentiated species of Tragulidae (Groves & Grubb 2011) stand in contrast to the overall pecoran species number of 200 to more than 300 (dependent on species concepts used). Moreover, the very differently sized Pecora (body masses from 2 kg in *Madoqua* to 1500 kg in *Giraffa*) inhabit nearly all terrestrial habitats from coast to high mountains and from equator to subpolar regions (Wilson & Mittermeier 2011), whereas all of the tragulids are of small size, and inhabit exclusively dense forest undergrowth or thickets within these forests in Africa and southeast Asia (Meijaard 2011). Although very few peer-reviewed reports on their natural diet exist (but *see* Dubost 1984), extant tragulids are commonly considered to be selective feeders with a major component of fruit and additional browse (Meijaard 2011). This is supported by a correlation of tragulid density with the abundance of fruit (Heydon & Bolloh 1997). In contrast, the fossil record of tragulids points to a diverse evolutionary history with a substantial diversification at the beginning of the Miocene or even end of the Oligocene (Geraads 2010, Sánchez *et al*. 2010). It documents a wide geographical distribution covering vast parts of Afro-Eurasia, large ranges of body sizes (more than twice the size of the largest extant species), skeletodental morphologies, preferred diets, and habitats as well as a common sympatric occurrence of up to four species in the Miocene (23.03 to 5.3 mya) (Mottl 1961, Fahlbusch 1985, Pickford 2001, Rössner 2004, 2007, Barry *et al*. 2005, Eronen & Rössner 2007, Kaiser & Rössner 2007, Ungar *et al*. 2012). In particular, dietary reconstructions for fossil tragulids indicate a spectrum that ranges from fruit-dominated to pure browse diets and mixed diets with a distinctive monocot component (Kaiser & Rössner 2007, Ungar *et al*. 2012); tragulids have therefore recently been considered ‘ecological precursors’ of bovid ruminants (Ungar *et al*. 2012).

The ruminant digestive system is characterised by a multi-compartmental forestomach that harbours a physiological sorting mechanism, followed by a glandular stomach that is the homologue of the simple stomach of other mammals (Clauss & Hofmann 2014). The morphology of the ruminant forestomach varies between ruminant species in many characteristics (Hofmann 1973, 1989, Clauss *et al*. 2006, 2009a, 2010b, Clauss & Hofmann 2014), but there is one major difference between the two infraorders of ruminants, the Pecora (in the modern world represented by families Bovidae, Moschidae, Cervidae, Giraffidae, Antilocapridae) and the paraphyletic “Tragulina” (in the modern world represented only by Tragulidae) (Fig. 1). The pecoran stomach represents the ruminant condition as known from domestic species: four functionally different compartments, comprising the rumen (the major site of microbial fermentation), the reticulum (the site of the sorting mechanism), the omasum (the site of re-absorption of fluid that is used for both the sorting mechanism and harvest of microbes from the rumen), and the abomasum (the glandular stomach) (Clauss & Hofmann 2014). In contrast, the stomach of tragulids only comprises three compartments — it is lacking the omasum (Milne-Edwards 1864, Schmidt 1911, Vidyadaran *et al*. 1982). The absence of the omasum in tragulids has been considered one of many anatomical traits that reflect either a basal phylogenetic position of tragulids among extant ruminants (Langer 1988) or a highly derived position with secondarily achieved primitive traits among pecorans (Boas 1890). The latter assumption has not found support in subsequent studies on ruminant phylogeny. The ruminant sorting mechanism in the reticulum depends on a high moisture content in this organ. Digesta with such a high moisture content is highly diluted. If such digesta would pass on into the abomasum, the abomasum would have to secrete high amounts of acid and gastric enzymes to compensate for that dilution. The addition of an omasum between the reticulum and the abomasum could therefore represent an advantage as it re-absorbs significant amounts of the moisture from the digesta.

Giraffidae, crown Pecora, and ruminant gestation periods

Opinions on the phylogenetic position of Giraffidae within crown Pecora have changed constantly before times of molecular/morphomolecular analyses (e.g. Gentry 1994, 2000, Hassanin & Douzery 2003). Meanwhile, there is broad consensus on the origin of Giraffidae laying within crown Pecora prior to all other included clades except Antilocapridae (e.g. Janis & Scott 1987, Hernández-Fernández & Vrba 2005, Hassanin *et al*. 2012). According to the fossil record (Harris *et al*. 2010), the African origin of giraffids (Gentry 2000) dates back at least to 19 mya (Solounias 2007). Giraffoid ancestors of giraffids could have originated from Eurasian stem pecorans (Gelocidae) before the Early Miocene. Coincidentally, molecular clock analyses produced dates of origin for giraffids in the Late Oligocene (Hassanin & Douzery 2003, Hassanin *et al*. 2012).

The nine currently differentiated species of Giraffidae (Brown *et al*. 2007, Groves & Grubb 2011) also stand in contrast to the overall number of crown pecoran species. The giraffe (*Giraffa* spp.), usually considered the largest extant ruminant (Clauss *et al*. 2003) with a body mass of up to 1500 kg, has a widespread distribution across subsaharan Africa savannas, and the unique feeding adaptation of a long neck that ensures a feeding niche not attained by any other ruminant (Cameron & du Toit 2007). In contrast, the okapi (*Okapia johnstoni*), with a body mass in the range of antelope at 250 kg, has a very limited distribution range in the Itulu forest of Zaire (Skinner & Mitchell 2011). Both genera are considered very strict browsers that nearly always avoid the intake of grass forage (Skinner & Mitchell 2011); both genera are also prime examples of brachydont ruminants (Janis 1988). Similarly as with the fossil record of tragulids, the fossil record of giraffids indicates a diverse evolutionary history with a substantial diversification during the Middle and Late Miocene (Gentry & Heizmann 1996, Harris *et al*. 2010), including a wide geographical distribution range in the Old World, a variety of skeletodental morphologies, preferred diets, and habitats as well as a common sympatric occurrence of up to four species in the Late Miocene (Gentry & Heizmann 1996, Harris *et al*. 2010). Although a characteristic feature of giraffids is the always comparably large body size among contemporaneous ruminants, there was, and still is between *Giraffa* and *Okapia*, a considerable body size diversity in this group (Solounias 2007). In particular, dietary reconstructions for fossil giraffids indicate a spectrum that covers the whole range from browsing to grazing (Solounias *et al*. 2000, 2010, Cerling *et al*. 2005).

Among the ruminants, giraffids are peculiar because of evident differences in life history: both the maximum longevity and the gestation time are distinctively longer in giraffids (Müller *et al*. 2011a, Clauss *et al*. 2014) (Fig. 2). Reasons

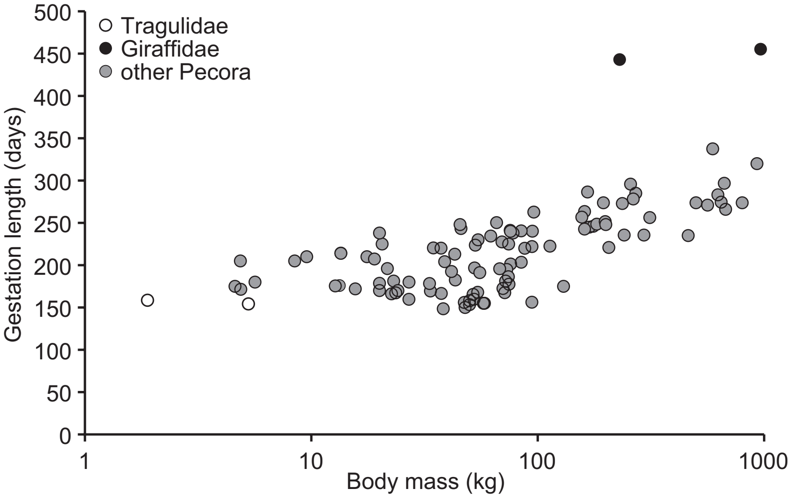

Fig. 2. Gestation periods in extant ruminants (cf. Müller *et al.* 2011a). Note the distinctively longer gestation periods in the two extant giraffids (*Okapia johnstoni*, *Giraffa camelopardalis*) as compared with other ruminants.

why giraffid newborns, which are of a similar degree of precociality as bovid or cervid newborns, require these dramatically longer gestation times for their development are, to our knowledge, unknown. Because short gestation times will reduce generation intervals, and may represent an important adaptation to seasonal environments (Zerbe *et al*. 2012), this difference could put giraffids at a disadvantage, both in terms of geographical range they can exploit competitively, and in niche competition with crown Pecora of shorter generation intervals.

Aim of this study

With this study, we aim at documenting the taxonomic distribution pattern of Old World-ruminants known so far through the Younger Cenozoic. Given the reasons to suspect a more efficient function of the forestomach in Pecora (with an omasum) than in tragulids (without an omasum), we expect that Pecora replaced tragulids during the course of evolutionary history. Hence, the ruminant fossil record should show a gradual shift of the taxonomic composition from a predominance of tragulids towards a clear dominance of pecoran families. Given the reasons to suspect a more efficient mode of reproduction in non-giraffid crown Pecora, we expect that these groups replaced giraffids during evolutionary history. Again, the fossil record should document a decline in the proportion of giraffid species with a parallel increase of the proportion of non-giraffid crown Pecora.

Material and methods

In order to provide a comparative frame for the analysis of pecoran/tragulid faunal composition over time, we compiled a data matrix of documented fossil ruminant species. Since tragulid origins are still debated (*see* above), we focused on reliably taxonomically allocated tragulids from the Afro-Eurasian Cenozoic and spatiotemporally coinciding Pecora.

The number of Old World ruminant species was compiled from the Miocene to the Holocene (exclusive Recent) by generation of species occurrences from the NOW database (Fortelius 2012). The master data matrix was downloaded on 23 May 2012. A split of this matrix into taxonomic data subsets follows basically the classification into families; some uncertain taxonomic cases were categorized as *Pecora indet*. The geographic regions Eurasia and Africa were treated individually. In doing so, the Arabian Peninsula was considered a part of Africa for the Miocene and a part of Eurasia in time intervals younger than the Miocene according to Popov *et al*. (2004). The master matrix and all the data subsets are available from the authors on request.

Absolute numbers of species were counted for the shortest time intervals possible to be differentiated when correlating the different age

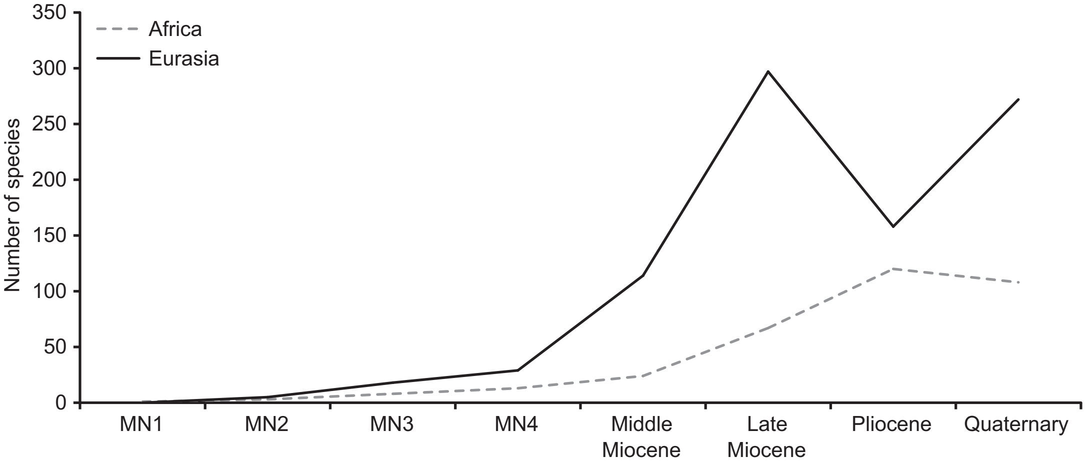

Fig. 3. Number of ruminant species recorded in different time intervals in Africa and Eurasia. For a definition of MN1–MN4, *see* Material and methods.

concepts used in NOW. Correlations of different age concepts were made using the literature (Qiu *et al*. 1999, Popov *et al*. 2004, Hilgen *et al*. 2012). Taxonomic data subsets were separated for time intervals Early Miocene (23.03 to 15.97 mya), Middle Miocene (15.97 to 11.63 mya), Late Miocene (11.63 to 5.33 mya), Pliocene (5.33 to 2.59 mya), Pleistocene (2.59 to 0.0117 mya), and Holocene (0.0117 to before Recent). In addition, we separated European Land Mammal Zones of the Neogene (MN zones) and correlates in Asia and Africa within the Early Miocene to obtain a higher resolution for the Early Miocene (because of the low species number in MN1 and MN2 (*see* Fig. 3), data were only evaluated from MN3 (~19.75 to ~18.0 mya) (Hilgen *et al*. 2012) and MN4 (~18.0 to ~16.9 mya) (Hilgen *et al*. 2012). We did not distinguish between earliest MN5 (Early Miocene) and the rest of MN5 (Middle Miocene) (Hilgen *et al*. 2012), but included all MN5 species in the Middle Miocene. Species with imprecise age indications were excluded from our analysis (e.g. "Miocene" or "MN4/MN6").

Species counts do not include taxa listed as "indet." or "sp." unless there is just a single one for the respective interval, in which case it was counted as the only species. Species listed as "indet." or "sp." were counted only when no other species of the same genus was listed for the same time interval. Genera listed as "indet." were counted only when no other genus was listed for the same time interval. "sp." was always preferred against "indet.". In the analysis we used the superordinate taxa Giraffoidea, Cervoidea (excluding Andegamerycidae and Palaeomerycidae) and Bovoidea as count categories in order to include several species which have only been identified more similar to one pecoran family than to another. Apart from some exceptions, we did not modify the taxonomic content of the data subsets. Exceptions are taxa listed in NOW as Giraffoidea (*Walangania*, "*Gelocus*" *whitworthi*, *Propalaeoryx*, *Prolibytherium*, *Sperrgebietomeryx*, *Orangemeryx*, *Namibiomeryx*, *Canthumeryx*), which have been revised as Pecora indet. (Gentry 1994, Cote 2010), and taxa listed in NOW as Moschidae (*Amphitragulus*, *Dremotherium*, *Pomelomeryx, Friburgomeryx*), which were excluded (Sánchez *et al*. 2010) and compiled as Pecora indet. here. Listings of tragulid *Dorcatherium naui* older than European Land Mammal Unit MN9 were considered *D. crassum* with the exception of Przeworno 1 and 2 (Czyżewska & Stefaniak 1994, *see* Alba *et al*. 2011). Late Middle Miocene *Dorcatherium naui* records from Abocador de Can Mata, Spain (Alba *et al*. 2011) and Gratkorn, Austria (Gross *et al*. 2011) are not yet included in NOW, but were taken into account. *D. rogeri* was considered constantly a synonym of *D. vindebonense* (Thenius 1952), as well as *D. libiensis* a synonym of *D. pigotti* (Geraads 2010). Further, we included additional information on occur-

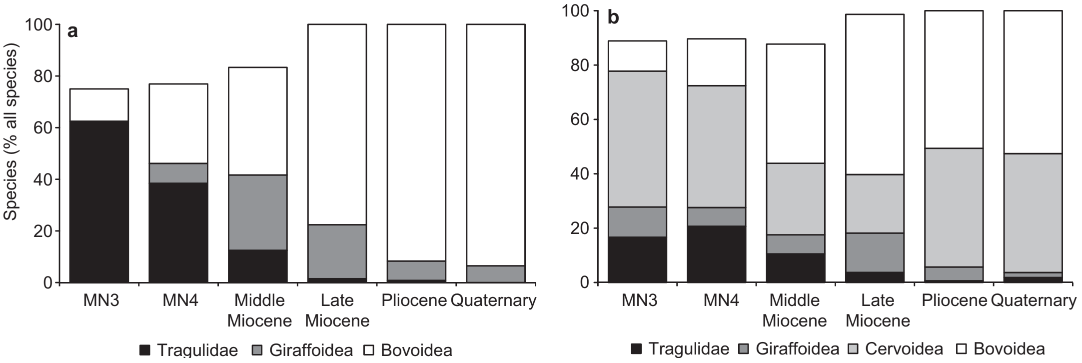

Fig. 4. Proportion (%) of species numbers of different ruminant groups recorded from different subsequent periods in (**a**) Africa and (**b**) Eurasia. The difference to 100% represents pecoran species with unknown higher taxonomical affiliation, species from extinct pecoran families, and insignificant Moschidae. *See* Material and methods for details.

rence and age of African tragulids from Pickford (2001), Geraads (2010), and Ungar *et al*. (2012).

Results

In general, the database inquiry provides species counts, which document a constantly increasing number of ruminants both in Africa and Eurasia during the Younger Cenozoic, with a peaking pattern of different magnitude in the two continents (Fig. 3), reflecting results from earlier studies (e.g. Gentry 1994, 2000, 2010a, 2010b, Gentry & Heizmann 1996, Gentry *et al*. 1999, Barry *et al*. 2005, Costeur & Legendre 2008, Bibi *et al*. 2009, Cote 2010, Geraads 2010, Harris *et al*. 2010, Bibi 2011). However, disparity in species numbers of the different ruminant groups is evident for all time spans differentiated. Whereas Bovoidea, Giraffoidea, and Cervoidea in general always dominated ruminant faunas [with the exception of tragulid predominance of African MN3 (Fig. 4a)], species of unknown pecoran allocation and extinct pecoran families (Andegamerycidae, Palaeomerycidae) decreased over time (missing species portion plus insignificant number of Moschidae represent difference to 100% in Fig. 4). Tragulidae represented substantial portions of the overall ruminant fauna in the Early/Middle Miocene (in accord with Pickford 2001, Eronen & Rössner 2007), but do not show such a significant species number predominance in the Early Miocene of Eurasia (Fig. 4b) as documented from Africa (Fig. 4a). In Africa (Fig. 4a), Bovoidea, and in Eurasia (Fig. 4b), Bovoidea and Cervoidea became dominant from the Middle Miocene onward, and Tragulidae decreased at the same time to very few species. The Giraffoidea had a general species diversity peak in the Middle/Late Miocene, but never reached Bovoidea or Cervoidea in species number and decreased in proportion afterwards (Fig. 4) as shown and discussed by Gentry and Heizmann (1996), Gentry (2000) and Costeur and Legendre (2008).

Discussion

Diversification sequence

The result of the database inquiry clearly displays the remarkable Early Miocene Old World radiation of crown Pecora, the different species diversity peaks and spatiotemporal abundance of Tragulidae, Cervoidea, Bovoidea, and Giraffoidea, as well as their predominance and replacements through the Cenozoic. With the exception of Bovoidea and Cervoidea in the Eurasian Pliocene and Quarternary, there is no evidence for a diversity balance between the different ruminant groups.

Indeed, the sequence of diversity peaks and the overall pattern reflect the nearly complete replacement of tragulids by Pecora within the Early and Middle Miocene, and of giraffids by cervids and bovids in the Pliocene, leaving just a handful of records for both groups in the

Holocene. This disparity necessarily implies a narrowing of the habitat range, which is supported by palaeodiet reconstructions for fossil tragulids, which cluster with living browsers and mixed feeders in contrast to frugivorous habits of living tragulids (Kaiser & Rössner 2007, Ungar *et al*. 2012), and by paleodiet reconstructions of fossil giraffids, which cover the whole browser to grazer spectrum, in contrast to the strict browse diet of extant species (Solounias *et al*. 2000, 2010, Cerling *et al*. 2005). In contrast to our expectations, only records from Africa produce a clear pattern of succession in terms of species majority, but not those from Eurasia. In Eurasia, the Pecora, and on a lower taxonomic level the bovids and cervids, always represented the highest proportion of species at any time investigated in this study. The major difference in the diversification sequences of Africa and Eurasia is the always significant proportion of cervids in Eurasia. If cervids remain unconsidered, a more or less similar diversification sequence is evident for Africa and Eurasia. With respect to the question of key innovations we wanted to answer, it appears as if the ‘superiority’ of the Pecora already shaped species diversity in Eurasia from the Early Miocene onwards as also described by Gentry (1994, 2000) — essentially driven by early cervid diversification. Morphophysiological differences especially between cervids and bovids, and potential explanations for their difference in modern ecological and geographical distribution ranges, are discussed elsewhere (Heywood 2010).

Explanations as narratives

An important limitation of this study is that no real test of the relevance of the omasum can be performed, due to the absence of other ungulate groups in which the course of species diversity over time in clades with a forestomach with and without an omasum-like structure can be compared. In extant organisms, a statistical evaluation of diversification rate and characters considered key innovations is possible (e.g. Bond & Opell 1998, Dumont *et al*. 2012); in the fossil record, such an evaluation is feasible if the character in question evolved in several different clades, such as the hypocone in mammalian molars (Hunter & Jernvall 1995). In the absence of such conditions, the major qualitative test of the hypothesis put forward is the plausibility of the argument (Jensen 1990, Rohde 1996). For this, the observation that clades without the key innovation covered a similar niche range, at least in terms of reconstructed diets, is important. Similar broad diet ranges mean that differences in diversification patterns cannot be easily explained by shifts in the proportion of habitats or resources available to ruminants, but must be sought in other factors (such as the proposed key innovations). Yet, the problem remains in accounting for the higher diversity of one group with a key innovation. One never knows if this one detail was really the key to success, or if there was a multitude of other factors. Ultimately, explanations for species diversity patterns as presented here must be considered (plausible) narratives (Carcraft 1990). With respect to the life history parameter used in our explanation (gestation period length), differences in other mammal groups, though beyond the scope of this study, could be used to test for a similarity in diversification sequence, with more recently radiated taxa having shorter gestation periods.

The ruminant forestomach

The major peculiarity of the ruminant forestomach is its sorting mechanism. It ensures that only small particles are passed out of the reticulum, whereas larger ones are retained. This depends on a density gradient of particles on the one hand (Baumont & Deswysen 1991, Lechner-Doll *et al*. 1991), and on the presence of a fluid environment in the reticulum on the other, in which density-based sorting by flotation and sedimentation can occur. Therefore, the reticulum contents are always particularly moist in ruminants (Clauss *et al*. 2009b, 2009c). When digesta is passed from the reticulum to the lower digestive tract, this digesta therefore will contain a high moisture content, which constitutes a dilution factor that will require a high secretion output in the subsequent stomach and intestinal regions. One of the major functions of the omasum as it is understood today is the absorption of fluid from the digesta that leave the reticulum (reviewed in Clauss *et al.* 2006). Correspondingly, the digesta in the omasum are invariably much drier than in the reticulum (Clauss *et al.* 2009b, 2009c) and also than in the subsequent glandular stomach, where acid and enzyme secretions increase the moisture content again. Notably, this fluid-reabsorption function should ***not*** be linked to a putative adaptation to dry environments; actually, those ruminant species with the largest omasum (cattle relatives; Clauss *et al.* 2006) are the ones that have the highest fluid loss in their faeces and thus defecate in 'pies' (Clauss *et al.* 2003, 2004). Rather than relating to the fluid homeostasis of the whole organism, the omasum is associated with the fluid regulation within the stomach complex. The addition of the omasum between the reticulum and the abomasum could therefore help reducing the workload on the secretory cells and thus represent an energy and protein saving mechanism.

Additionally, the omasum might allow ruminants to evolve a high-fluid throughput strategy through the reticulorumen that is a characteristic of the so-called 'cattle-type' ruminants (Clauss *et al.* 2010a). The additional benefit of this high fluid throughput was first suspected to lie in the formation of a 'fibre raft', and the associated increased efficiency of the sorting mechanisms and a 'filter bed-effect' that delays the excretion of small particles and thus facilitates an even more efficient digestion (Clauss *et al.* 2008). However, it could be shown that the efficiency of the sorting mechanism does not differ in a relevant way between 'moose-type' ruminants with a low, and 'cattle-type' ruminants with a high, fluid throughput (Lechner *et al.* 2010). Correspondingly, tragulids, whose fluid passage pattern in the forestomach matches that of 'moose-type' ruminants (Darlis *et al.* 2012), do not stand out among ruminants in terms of faecal particle size reduction (Clauss *et al.* 2002). But, the important additional advantage of a high fluid throughput through the forestomach could lie in the additional harvest of microbes that are washed out at a high rate (Hummel *et al.* 2008, Clauss *et al.* 2010a, Müller *et al.* 2011b). Thus, more microbes reach the abomasum and small intestine per unit time, where they are digested. By the higher harvest rates, the ruminal microbe pool is manipulated towards higher growth rates, and is therefore utilized more efficiently. Such a strategy may only be feasible if an omasum prevents the negative dilution effects of a high forestomach fluid throughput. Notably, a 'moose-type' strategy does not prevent animals from ingesting grass or mixed grass/browse diets in an experimental setting (Lechner *et al.* 2010) or when no other competitors are present. For example, the reindeer is an outlier to a general pattern, because its natural diet includes much more grass than one would expect based on its 'moose-type' rumen physiology (the major outlier in the dataset of Codron & Clauss 2010); this species hardly faces competition from sympatric grazers. In most real ecological settings, 'moose-type' ruminants are limited to browse-dominated diets, whereas 'cattle-type' ruminants dominate grass or mixed grass/browse diet niches (Codron & Clauss 2010). This difference matches the observed reduction of the tragulid niche to that of 'moose-type' ruminants.

Gestation period

Gestation period is an important life history measure that contributes to the overall reproduction potential of a species. Shorter gestation periods are commonly linked to shorter generation intervals, or to a higher maximum population growth rate, and gestation period can therefore serve, to a limited extent, to characterise species' life history on a 'slow-fast continuum' (Bielby *et al.* 2007). In general, given ecological similarity between species under no particular resource constraint, one would expect a faster-reproducing species to 'outcompete' a slower one. Additionally, the length of the gestation period is relevant for reproduction in seasonal environments, as it will determine if species can reproduce in synchrony with seasonal variation without losing reproductive potential (Kiltie 1988, Owen-Smith 1988). Modifications of gestation period might therefore be part of a set of adaptations that facilitates the invasion of new, more seasonal, environmental niches (Zerbe *et al.* 2012). Although the length of the gestation period can vary intraspecifically with a variety of factors (reviewed in Clements *et al.* 2011), gestation period is a reliable species-specific measure that allows inter-specific comparisons (Ogutu *et al*. 2010, Clements *et al*. 2011).

The long gestation periods observed in giraffids exceed one year. This makes giraffids the only pecoran group that is unable to adopt a seasonal breeding pattern (that would be advantageous in more temperate climates) without losing breeding potential due to longer periods of reproductive inactivity (Zerbe *et al*. 2012). The fact that giraffid diversity was proportionally lower in Eurasia, with a putatively more temperate climate, than in Africa (e.g. Bruch *et al*. 2007), supports the interpretation that they might be less successful in seasonal environments (Fig. 4). The suggested advantage of shorter gestation periods in bovids and cervids does not only apply to the comparison of these clades to giraffids, but also to perissodactyls, especially equids (Grange & Duncan 2006), and camelids (Clauss *et al*. 2014). This life history characteristic might therefore have played an additional role — apart from the differences in digestive morphophysiology mentioned in the Introduction — in large mammalian herbivore species diversification patterns. As mentioned above, it would be interesting to check whether more recently diversified taxonomic groups of other clades also have comparatively shorter gestation periods. Notably, the morphophysiological mechanisms behind such life history differences remain to be identified.

‘Increased fitness’ key innovations

The key innovations mentioned in this study belong to the group of ‘increased fitness’ key innovations *sensu* Heard and Hauser (1995); such innovations do not open a particular new niche or lead to increased specialisation (as would ‘new adaptive zone’ or ‘specialisation’ innovations), but increase the general efficiency of organismal function. A typical feature of such innovations is that the clade that diversified (due to that innovation) does not necessarily occupy a new or specialised niche but covers a similar broad niche spectrum as its predecessors, or an even broader one. Examples for such innovations are the mammalian molar hypocone (Hunter & Jernvall 1995), ungulate hypsodonty (Feranec 2007), the evolution of a ‘cattle-type’ rumen physiology with a high fluid throughput through the rumen (Codron & Clauss 2010), and maybe also short gestation periods (Clauss *et al*. 2014). One characteristic of these increased fitness key innovations yet to be proven is that they are not costly during ontogeny or life. This would limit them to specific environmental conditions. Another characteristic of such ‘increased fitness’ key innovations scenarios is that apparent ‘specialists’ remain of the preceding pre-innovation clades, such as the brachydont, omasum-free tragulids, or the brachydont, long gestation period giraffids, or ‘moose-type’ ruminants with a low fluid throughput through the rumen in general. The parsimonious interpretation is that these specialists inhabit niches in which the key innovation cannot take effect, either because it does not offer a selective advantage in that peculiar niche, or because this niche requires particular adaptations that cannot be reconciled with the key innovation (McNabb 2012). In the case of the remaining, small-bodied tragulids, the putative disadvantage of a lacking omasum may not come into play in the strictly frugivorous/browsing niche, because ruminants in that niche depend on saliva rich in tannin-binding proteins. The production of such saliva possibly precludes the production of the high saliva volumes necessary for a high fluid throughput strategy (Hofmann *et al*. 2008, Clauss *et al*. 2010a, 2011, Codron & Clauss 2010). Without an omasum, tragulids could thus survive in diet niches otherwise occupied by ‘moose-type’ ruminants such as duikers (Clauss *et al*. 2011). Extant giraffids survive in their unique feeding niches, either because of their long neck and associated morphophysiological adaptations that are unique in ruminants (Cameron & du Toit 2007, Mitchell & Skinner 2010) in the case of the giraffe, or because of historical contingency in the Itulu forest in the case of the okapi. Identifying the conditions that allow those species not endowed with a key innovation to persist in their niches is an important part of explaining the relevance of key innovations.

Conclusion

To conclude, this study provides a plausible but not exhaustive narrative that explains the sequence of diversification and evolutionary disparity patterns in ruminants from the beginning of the Neogene to Extant, with an emphasis on innovative characters of digestive morphophysiology and life history. A similar ruminant specific diversification sequence can be derived from the data collection in Jardine *et al*. (2012) for a longer time span in North America, with a peak of traguloid species diversity in the Eocene and a subsequent decline and concomitant increasing diversity of Pecora from the Oligocene onward. Obviously, it would be interesting to compare ruminant diversity patterns in earlier time periods in the Old World.

Whereas the tragulid forestomach anatomy may have conserved an earlier developmental stage of the digestive tract in ruminant evolution, the pecoran forestomach added the omasum. This difference in the overall efficiency of the forestomach may have made tragulids susceptible to resource competition in the context of increased openness of landscapes during the Neogene, and their fall a contemporaneous event to the initial major diversification of pecorans. The omasum, a hallmark of the pecorans, and especially developed in the most recently radiated bovids, may well be the decisive innovation that sets the ruminant digestive strategy apart from that of other herbivores. Tragulids only survived in forested relic areas in which a frugivorous diet is possible year-round. Here, the pecoran's advantage will not be as pronounced as on grass or browse-dominated diets. Thus, today's frugivorous adaptation of tragulids does not necessarily represent an ancestral (living fossil) state of this clade, an often-stated view (e.g. Janis 1984, Thenius 2000), but rather a secondary restriction (in correspondence with Ungar *et al*. 2012).

For reasons unknown, extant giraffids have particularly long gestation periods compared to other ruminants. Whether this life history parameter is the proxy for a basic physiological difference remains unknown to date. Giraffids survive only either in a peculiar geographic niche [that may well represent a secondary niche into which the species had to retreat (Thenius 1992)] in the case of the okapi, or a peculiar feeding adaptation (Cameron & du Toit 2007) in the case of the giraffe.

The example of the differently speciose groups in different geographical regions — bovids only in Africa, and bovids and cervids in Eurasia — indicate that apart from processes linked to key innovations, biogeographical distribution also needs to be included in the explanation of species diversification patterns. The cause of the obviously significant ecological role of cervids in Eurasia, which had an immense impact on tragulid and giraffid radiation, is unknown yet.

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