geodiversitas

2019 • 41 • 10

Hungry for fruit? – A case study on the ecology of middle Miocene Moschidae (Mammalia, Ruminantia)

Manuela AIGLSTORFER &
Gina M. SEMPREBON

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

art. 41 (10) — Published on 9 May 2019
www.geodiversitas.com

Couverture / *Cover* :
Life reconstruction of *Micromeryx* Lartet, 1851 (based on male skeleton of *Micromeryx*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017; © SMNS).

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
– Science Citation Index Expanded (SciSearch®)
– ISI Alerting Services®
– Current Contents® / Physical, Chemical, and Earth Sciences®
– Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
– BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par / *Articles and nomenclatural novelties published in* Geodiversitas *are referenced by:*
– ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie.***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Hungry for fruit? – A case study on the ecology of middle Miocene Moschidae (Mammalia, Ruminantia)

Manuela AIGLSTORFER
Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart (Germany)
manuela.aiglstorfer@smns-bw.de (corresponding author)

Gina M. SEMPREBON
Bay Path University, 588 Longmeadow St, Longmeadow, MA 01106 (United States)
gsempreb@baypath.edu

Submitted on 10 September 2018 | accepted on 31 December 2018 | published on 9 May 2019

urn:lsid:zoobank.org:pub:4E9D136F-A463-465B-9733-3239F1DE9A97

Aiglstorfer M. & Semprebon G. M. 2019. — Hungry for fruit? – A case study on the ecology of middle Miocene Moschidae (Mammalia, Ruminantia). *Geodiversitas* 41 (10): 385-399. https://doi.org/10.5252/geodiversitas2019v41a10. http://geodiversitas.com/41/10

ABSTRACT
This study reveals the oldest fruit enriched diet in Moschidae so far. It deals with tooth meso- and microwear of *Micromeryx flourensianus* Lartet, 1851 and *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 from the two fossil-rich middle Miocene localities, Sansan (France, 14.1 Ma) and Steinheim am Albuch (a. A., Germany, 13.5 Ma). In combination with literature data it indicates different levels of frugivory in moschids during the Miocene and suggests ecologic niche partitioning of two sympatric moschids in Steinheim a. A. The Miocene data imply a dietary shift during the evolution of the family, as feeding on fruits and/or nuts is not common in modern Moschidae. A direct comparison of the results for Sansan and Steinheim a. A. points to a slightly more abrasive diet in Steinheim a. A. and thus assumedly more arid conditions. Differences are only minor, however, and indicate that Sansan was most likely already affected as well by the middle Miocene cooling phase.

KEY WORDS
Micromeryx,
microwear,
mesowear,
sympatry,
Middle Miocene cooling,
Miocene Climatic Event,
Steinheim am Albuch,
Sansan.

RÉSUMÉ
Une envie de fruits? – Étude de l'écologie des Moschidae (Mammalia, Ruminantia) du Miocène moyen.
Cette étude révèle les plus anciens Moschidae ayant un régime alimentaire en fruits. La méso- et la micro-usure dentaire de *Micromeryx flourensianus* Lartet, 1851 et *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 des localités de Sansan (France, 14,1 Ma) et Steinheim am Albuch (a. A., Allemagne, 13,5 Ma) ont été étudiées. La comparaison de ces données à d'autres du Miocène nous informe sur les différents niveaux de frugivorie au sein des Moschidae. Elle suggère une partition des niches écologiques entre les deux espèces sympatriques de Steinheim a. A. Les données du Miocène impliquent un changement dans le régime alimentaire au cours de l'évolution de cette famille, puisqu'il n'est pas commun, pour les Moschidae actuels, de se nourrir de fruits et/ou de noix. La comparaison entre les sites de Sansan et Steinheim a. A. indique une nourriture plus abrasive chez les spécimens de Steinheim a. A. et donc des conditions environnementales supposées plus arides. Cependant, les différences sont mineures, la localité de Sansan étant probablement déjà affectée par la phase de refroidissement du Miocène moyen.

MOTS CLÉS
Micromeryx,
méso- et micro-usure dentaire,
sympatrie,
refroidissement du Miocène moyen,
évènement climatique du Miocène,
Steinheim am Albuch,
Sansan.

INTRODUCTION

Moschidae are small pecoran ruminants with elongated upper canines in the males and a lack of cranial appendages. Once spread all over Eurasia with several genera, the family is now reduced to one genus only – *Moschus* Linnaeus, 1758. Today *Moschus* comprises six endangered (*M. anhuiensis* Wang, Hu, & Yan, 1982; *M. berezovskii* Flerov, 1929; *M. chrysogaster* Hodgson, 1839; *M. cupreus* Grubb, 1982; *M. fuscus* Li, 1981; *M. leucogaster* Hodgson, 1839), and one vulnerable species (*M. moschiferus* Linnaeus, 1758) (IUCN 2018). It is restricted to mountainous regions of Asia, mainly in the Palearctic (*sensu* Wallace [1876]) and Sino-Japanese zoogeographic realm (*sensu* Holt *et al.* [2013]), and often lives in areas where the ground is covered with snow more than half of the year (Green 1986; Green & Kattel 1997; Groves 2011; Pan *et al.* 2015).

The phylogenetic position of the moschid family has been the subject of debate for long, and at the moment, they appear to be most likely the sister group of bovids (Webb & Taylor 1980; Janis & Scott 1987; Vislobokova 1990; Gentry 1994; Su *et al.* 1999; Gentry 2000; Hassanin & Douzery 2003; Hernández Fernández & Vrba 2005; Vislobokova & Lavrov 2009; Sánchez *et al.* 2010, 2015; dos Reis *et al.* 2012; Hassanin *et al.* 2012; Bibi 2013, 2014). As the split of moschids and bovids is assumed to have taken place more than 20 Ma ago (Mennecart *et al.* 2012, 2017, 2018; Sánchez *et al.* 2015), modern *Moschus* can be considered a terminal taxon of a long isolated lineage and by itself can offer only a very limited data set that is highly susceptible to homoplastic features. Thus, by studying the fossil moschid record we can essentially improve our understanding of the family, especially its early evolution and in-detail phylogeny. By doing this, we also expect to gain better understanding of the ecological plasticity in moschids throughout their evolution: Is modern moschid ecology the relic of a once wider and more diverse ecology or does it represent a completely new trait?

During its evolutionary history, the family represented a common faunal element in the Miocene terrestrial communities of Eurasia (Vislobokova 2007; Sánchez & Morales 2008; Sánchez *et al.* 2009; Vislobokova & Lavrov 2009; Sánchez *et al.* 2010, 2011; Aiglstorfer & Costeur 2013; Aiglstorfer *et al.* 2014b, 2017, 2018; Wang *et al.* 2015). Currently, three fossil moschid genera are considered valid (*Micromeryx* Lartet, 1851, *Hispanomeryx* Morales, Moyà-Solà & Soria, 1981, *Moschus*), while other taxa such as *Amphitragulus* Croizet *in* Pomel, 1846, *Pomelomeryx* Ginsburg & Morales, 1989, *Bedenomeryx* Jehenne, 1988, *Dremotherium* Saint-Hilaire, 1833, and the northern American Blastomerycinae seem to belong to other lineages (Sánchez *et al.* 2010, 2015; Mennecart 2012; Mennecart *et al.* 2012; Aiglstorfer *et al.* 2017; Mennecart *et al.* 2018).

Geographic, stratigraphic and taphonomic setting

In this study, we focus on one of the oldest moschid species and the type species of *Micromeryx* (see Fig. 1 for a life reconstruction of *Micromeryx*): *Micromeryx flourensianus* Lartet, 1851. This species was present in European ecosystems from the middle Miocene to the early late Miocene (at least from about 15/16 Ma to 11 Ma; Aiglstorfer *et al.* 2018). There are two localities with a rich fossil record of this taxon: the type locality of the species, Sansan (France), and the locality Steinheim am Albuch (a. A.; Germany) (Fig. 2). Both localities are of middle Miocene age and can be assigned to a time period which marks the change from the Miocene Climatic Optimum (about 17 to 15 Ma; Kovar-Eder & Teodiris [2018]) to the subsequent Middle Miocene Cooling phase/"Miocene Climatic Event" that led to more arid conditions and stronger seasonality in Central and Western Europe.

Sansan (reference locality for MN6) is located in the molasse de l'Armagnac (Ginsburg & Bulot 2000) in the South of France. The age of the locality was originally considered to be about 15 Ma (Sen & Ginsburg 2000). Several works have argued for a younger age of the locality and at the moment an age of 14.1 Ma is considered the most likely (Hilgen *et al.* 2012). Steinheim a. A. is stratigraphically and biochronologically more recent. It is located on the karstic plateau of the eastern part of the Swabian Alb (SW Germany) and comprises middle Miocene lake sediment in-fills of a crater that formed during a binary asteroid impact between 14.6 and 15.0 Ma ago (Stöffler *et al.* 2002; Buchner *et al.* 2013). The higher layers of the lake sediments, roughly considered to be about 13.5 Ma (Tütken *et al.* 2006), are rich in mammal remains (Heizmann & Reiff 2002) and represent the reference locality of the Neogene Mediterranean Mammal Unit MN7. Steinheim a. A. has delivered the worldwide richest fossil moschid material so far and houses a second moschid taxon, *Micromeryx*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017, besides *M. flourensianus* (Aiglstorfer *et al.* 2017).

The faunal records of both localities can be considered as palaeocommunities without any mixing in terms of stratigraphy, and moschid specimens were not accumulated in secondary lagerstätte. We can assume an autochthonous taphocoenosis for the locality Steinheim a. A.: lake sediments, no indication for water currents, articulated skeletons, and no signs for abrasion (Heizmann & Reiff 2002; Tütken *et al.* 2006). The main accumulations of plants, mammals and non-mammalian vertebrates are not from the same horizon in Steinheim a. A. and may have recorded slightly different environmental conditions. However, as there are no floral or faunal indications for distinct environmental differences of the lake surroundings in between the main fossil bearing horizons, we consider it justified to reconstruct the assemblage as a whole in terms of a time-averaged palaeoecosystem (Heizmann & Reiff 2002).

For Sansan, Aiglstorfer *et al.* (2019) reconstructed the moschid accumulation as an allochthonous / suballochthonous assemblage strongly influenced by carnivore activity and with an impact of fluvial transport. Although we are aware that the faunal assemblage from Sansan represents a time-averaged community as well (Sen & Ginsburg 2000), the sedimentological and taphonomic history still allows an interpretation of the accumulation as a whole (Plaziat & Baltzer 2000).

Taking into account body size (3-6 kg for *M. flourensianus* [Aiglstorfer *et al.* 2014b; Aiglstorfer *et al.* 2019], between 6.5 and 8 kg for *Micromeryx*? *eiselei* (estimated after Damuth [1990], Janis [1990], and Scott [1990]) and the behavioural ecology of modern moschids, we consider the moschids from both locali-

Fig. 1. — Life reconstruction of *Micromeryx* Lartet, 1851 (based on male skeleton of *Micromeryx*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017; © SMNS).

ties as permanent inhabitants of the wider surroundings of the respective locality with a small radius of movement and not undertaking long migrations. Therefore, palaeoenvironmental data of the localities do indeed reflect frame conditions for the respective moschid habitats.

Aim of the study

For our study, we compare the two palaeopopulations of *Micromeryx flourensianus* from Sansan and Steinheim a. A., *M.*? *eiselei* (so far endemic to Steinheim a. A.), and the modern *Moschus* using mesowear and microwear in order to track ecological variation in terms of long- and short-term dietary behavior.

MATERIAL AND METHODS

Material

We sampled two Miocene moschid species from two localities: *M. flourensianus* from Sansan (eight specimens: MNHN.F.SA2970, MNHN.F.SA2971, MNHN.F.SA3812, MNHN.F.SA3813, MNHN.F.SA3817, MNHN.F.SA9772, MNHN.F.SA10973, MNHN.F.SA10971) and Steinheim a. A. (10 specimens: SMNS 15776 [not included in mesowear due to broken tip in paracone], SMNS 40252 [not included in mesowear due to broken tip in paracone], SMNS 40322, SMNS 42636, SMNS 42723 [not included in mesowear due to broken tip in paracone], SMNS 42925 [not included in mesowear due to advanced age], SMNS 46082, NMB Sth. 834, NMB Sth. 836, NMB Sth. 855 a), as well as *M.*? *eiselei* (two specimens for microwear: SMNS 40617 [old individual], NMB Sth. 833 [old individual]; four specimens for mesowear: SMNS 40617, NMB Sth. 833, NMB Sth. 825 [young individual], SMNS 40010 [young individual]) from Steinheim a. A. Furthermore, we included four recent specimens of *Moschus moschiferus* from Siberia (ZFMK 1997.664 and ZFMK 1997.666; SMNS 143 and SMNS 1238 [assignation and regional origin with reservations for the latter]) in our study.

TABLE 1. — Mesowear results for *M. flourensianus* Lartet, 1851, *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 (young) and *Moschus* Linnaeus, 1758. Abbreviations: **%S**, percentage of individuals with sharp mesowear; **%R**, percentage of individuals with rounded mesowear; **%B**, percentage of individuals with blunt mesowear; **%HR**, percentage of individuals with high mesowear relief; **%LR**, percentage of individuals with low mesowear relief.

		Mesowear values				
Locality and species	n	%S	%R	%B	%HR	%LR
Sansan (14.1 Ma)						
Micromeryx flourensianus	8	37.5	62.5	0	100	0
Steinheim (13.5 Ma)						
Micromeryx flourensianus	6	0	100	0	100	0
Micromeryx? *eiselei*	2	100	0	0	100	0
Siberia (modern)						
Moschus moschiferus	4	0	100	0	100	0

The material of *Micromeryx flourensianus* from Sansan has not been fully revised so far, and the species indeed still lacks the designation of a lectotype. However, in our study we did not find clear indications for the presence of a second taxon in the locality, and all specimens analysed in this study are well in accordance with intraspecific variability of one species.

METHODS

Terminology for dentition follows Bärmann & Rössner (2011).

Following Solounias & Semprebon (2002), we differentiated the following major herbivore dietary classes: grazer, leaf browser, mixed-feeder, and fruit/seed browser (the latter also summarized as frugivore in our study). Furthermore, we considered lichen-feeding (lichenophagy).

Tooth mesowear analysis

For mesowear analysis, we analysed the labial side of upper molars macroscopically, with a focus on the paracone of the M2 (due to bad preservation of M1 and M2 in the specimen only M3 could be analysed for SMNS 40010) following Fortelius & Solounias (2000). With this method, the gross dental wear of ungulate molars is characterized by the relief and sharpness of cusp apices and correlated with the relative amounts of attritive and abrasive dental wear. A less abrasive diet (i.e., high attrition) results in sharpened apices, while a more abrasive diet forms more rounded and blunted labial cusp apices. We used the variables: "%sharp", "%rounded", "%blunt", "%high relief" and "%low relief" for the summary statistics and "%sharp", "%rounded", "%blunt", and "%high relief" for the cluster analysis. We chose to use the original mesowear method of Fortelius & Solounias (2000) rather than the Mihlbachler *et al.* (2011) "ruler" constructed using extant *Equus* tooth cusps as a comparative standard (combining both occlusal relief and cusp shape into a single variable) as the occlusal relief in ruminant artiodactyls such as *Micromeryx* is often much higher than what is seen in perissodactyls and, therefore, accurate comparisons using the "ruler" may at times be difficult. We employ the mesowear technique here mainly as an index of relative abrasion incurred through dietary items rather than as a means to detect dietary classification per se. Rivals *et al.* (2007) have shown that mesowear is not as stable throughout the adult lifespan in brachydont versus mesodont and hypsodont species when used to predict dietary classification (although *Micromeryx* is higher crowned than clearly brachydont species, the tooth crown in the genus is lower than in *Rangifer*, used as representative of a mesodont taxon in the study by Rivals *et al.* [2007]).

Tooth microwear analysis

Microwear features of dental enamel on the paracone of the upper M2 (preferably from the left side) were examined with a stereomicroscope on high-resolution epoxy casts of teeth following the cleaning, moulding, casting and examination protocol developed by Solounias & Semprebon (2002) and Semprebon *et al.* (2004). Casts were observed using a light stereomicroscope (Zeiss Stemi 2000C) at 35× magnification by a single experienced observer (GS) to minimize error that may be incurred. As detailed in Solounias & Semprebon (2002), the refractive properties of the enamel microfeatures were employed to visualize food scars. Microwear scars (i.e., elongated scratches and rounded pits) were quantified in two areas on the paracone of the upper second molars in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias & Semprebon (2002) and Semprebon *et al.* (2004) which distinguish various types of pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, whereas scratches are elongated microfeatures that are not merely longer than they are wide, but have straight, parallel sides.

These scar categories are subdivided qualitatively as follows using their differential light refractive properties:

– Pits are classified as either small pits, large pits or puncture pits. Large pits are deeper, less refractive (always dark), generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits – the latter also are always bright and highly refractive. Puncture pits are large and very deep pits with crater-like features with regular margins and they appear dark due to low refractivity;

– Scratches are distinguished as either fine (i.e., narrow scratches that appear relatively shallow and have moderate refractivity – i.e., look white but relatively dim), coarse (i.e., wide scratches that are also relatively deep but have high refractivity – look brilliantly white) and hypercoarse (i.e., very deep and trench-like features that are wider than the other types of scratches and dark due to low refractivity);

– Gouges are features that have ragged, irregular edges and are much larger (approximately 2-3 times as large) and deeper than large pits. They are relatively dark features with low refractivity. The presence or absence of gouges in the microscope field was recorded.

Average numbers of scratches and pits allow for discrimination between the dietary categories of leaf browser (i.e., eating woody and non-woody dicotyledonous plants) vs grazer (i.e., eating grass). Animals that alternate between feeding on leaves and grass or on leaves and fruit show a wider variation in scratch/pit results (often falling in the gap between leaf browser and grazer scratch/pit ecospaces and display both high and low individual raw scratch results. In addition, taxa that enrich a folivore diet with a considerable amount of hard

and soft fruits, seeds, and nuts, termed as fruit/seed browsers (frugivores) generally display higher numbers of scratches than found in leaf browsers and higher percentages of coarsely or mixed types of scratches rather than the large percentage of finely textured scratches found in folivores. In addition, many individual specimens in these taxa show more than four large pits. Furthermore, the large pits seen in this group are very characteristic and unique. That is, they are the deepest pits observed (puncture-like and very symmetrical).

ABBREVIATIONS

MAP	Mean Annual Precipitation;
MAT	Mean Annual Temperature;
MN	Mediterranean Neogene Mammal Unit ;
MNHN.F	Muséum national d'Histoire naturelle, Paris, collection de Paléontologie;
NMB	Naturhistorisches Museum Basel, Basel;
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart;
ZFMK	Zoologisches Forschungsmuseum König, Bonn.

RESULTS

TOOTH MESOWEAR ANALYSIS

For the mesowear, we observe a high relief for *Micromeryx flourensianus* from both localities, as well as mostly rounded (Sansan) to completely rounded (Steinheim a. A.) cusps, displaying also a certain change in mesowear pattern along the life span (Table 1; Fig. 3). In the cluster analysis, *M. flourensianus* from Steinheim a. A. clusters with non-extreme grazers and the frugivores *Cephalophus silvicultor* (Afzelius, 1815), *C. natalensis* A. Smith, 1834 and *Hyemoschus aquaticus* (Ogilby, 1841). *M. flourensianus* from Sansan has less abrasive mesowear and clusters with extant mixed feeders and other *Cephalophus* H. Smith, 1827 taxa (Fig. 4). The cluster analysis shows that *Micromeryx flourensianus* does not have a mesowear signature that groups it with extant leaf browsers but has rather a higher level of abrasion than what is seen in extant leaf browsers.

The mesowear is more heterogenous in *Micromeryx*? *eiselei*. In the older individuals (SMNS 40617, NMB Sth. 833), the cusp shape is less sharp, which may indicate that the long-term diet included some fruit, but also (and more likely) could simply reflect more worn cusps due to advanced age. Consequently, we did not include old individuals of *M.*? *eiselei* in the cluster analysis or in Table 1 since their cusps might be expected to be worn due to age obscuring any normal dietary behavior. However, we did include the mesowear results from two young individuals of *M.*? *eiselei* in our cluster analysis as we found their highly attritive results more significant.Wear facets were present on their paracone enamel bands indicating some adult foods were likely being consumed. The two younger specimens (NMB Sth. 825, SMNS 40010) have sharp cusps and high relief typical of leaf browsers (Fig. 3) and thus cluster in Figure 4 with extant leaf browsers (e.g. *Alces alces* (Linnaeus, 1758)).

For modern *Moschus* from Siberia, we observed a high mesowear relief and rounded cusps comparable to *M. flourensianus* (Table 1). Modern *Moschus* clusters with *M. flourensianus* from Steinheim a. A. in the analysis (Fig. 4).

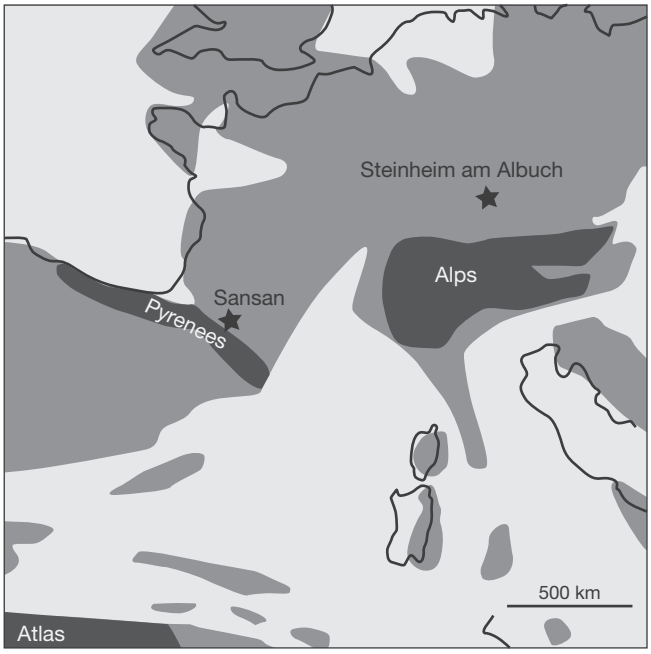

FIG. 2. — Geographic position of the middle Miocene localities Sansan (France) and Steinheim am Albuch (Germany); palinspastic map for the middle Miocene in Central and Western Europe modified after Neubauer *et al.* (2015).

TOOTH MICROWEAR ANALYSIS

For *Micromeryx flourensianus* from Sansan (n = 8) the number of pits ranges from 27 to 45 per counting area, for *M. flourensianus* from Steinheim am Albuch (n = 10) from 35 to 64. The number of scratches per counting area ranges from 7 to 22 for *M. flourensianus* from both localities. Many specimens have large pits, some of these are deep and puncture-like (Fig. 5B, D), and many individuals fall in between the extant leaf browsing and grazing morphospace (Fig. 6). Both results are typical for extant species that incorporate fruit and seeds in their diet. Only some individuals have very few large pits, lack puncture-like pits, and have results typical of more leaf browsing (Fig. 5A). *M. flourensianus* individuals from Steinheim a. A. have more pits overall and more large pits and gouges than those from Sansan (Table 2; Figs 5D, 7A). Furthermore Steinheim a. A. has more individuals with scratch numbers in or closer to the leaf browsing range (Fig. 6). Also, some individuals from Steinheim a. A., display a mixture of coarse and hypercoarse scratches (Fig. 7B).

The number of pits in *M.*? *eiselei* from Steinheim a. A. (older individuals; n=2) ranges from 30 to 42 and the number of scratches from 8 to 10 per counting area. Both specimens only show fine scratches and totally lack gouges (Table 2; Fig. 5C).

In order to compare our fossil data with modern *Moschus*, we sampled four available specimens (Fig. 5E, F). In our analysis, the numbers of pits range from 49 to 54, and scratches from 12 to 20 per counting area. Most specimens fall in between the extant leaf browsing and grazing morphospace (Fig. 6). Large pits are present in all specimens, three out of four specimens show clear gouges, and in all except one specimen, scratches are coarse and hypercoarse (Table 2; Fig. 7A, B). In contrast to the other individuals, the latter shows puncture-like pits and mixed scratches (Table 2; Fig. 5E).

TABLE 2. — Microwear results for *M. flourensianus* Lartet, 1851, *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 (old) and *Moschus* Linnaeus, 1758. Abbreviations: **n**, number of specimens; **NP**, total number of pits; **NLP**, number of large pits; **NS**, total number of scratches; **%LP**, percentage of individuals with large pits (if more than four large pits, coded as present in the specimen); **%PP**, percentage of individuals with puncture pits; **%FS**, percentage of individuals with fine scratches; **%MS**, percentage of individuals with mixed scratches; **%CS**, percentage of individuals with coarse scratches; **%C&HC**, percentage of individuals with coarse and hypercoarse scratches; **%G**, percentage of individuals with gouges; **SWS**, scratch width score: **0**, fine; **1**, mix of fine and coarse; **2**, coarse; **3**, mix of coarse and hypercoarse; **S/P**, scratch/pit ratio.

		Microwear values											
Locality and species	**n**	**NP**	**NLP**	**NS**	**%LP**	**%PP**	**%FS**	**%MS**	**%CS**	**%C&HC**	**%G**	**SWS**	**S/P**
Sansan (14.1 Ma)													
Micromeryx flourensianus	8	35.06	7.88	17.25	62.5	62.5	12.5	50	25	12.5	25	1.38	0.49
Steinheim (13.5 Ma)													
Micromeryx flourensianus	10	48.80	12.3	15.15	90	80	10	50	10	30	70	1.60	0.31
Micromeryx? *eiselei*	2	35.75	4	9	0	0	100	0	0	0	0	0	0.25
Siberia (modern)													
Moschus moschiferus	4	51.13	11.13	15.88	100	25	0	25	0	75	75	2.5	0.31

DISCUSSION

DIET OF MODERN AND FOSSIL MOSCHIDAE

Diet of Miocene Moschidae

Based on the relatively abrasive signature in the mesowear of *M. flourensianus* from Sansan and Steinheim a. A. we reconstruct that it was most likely not feeding on soft leaves exclusively but included some seed/fruit in its diet as fruit consumption has been shown to cause rounding of molar cusps (Fortelius & Solounias 2000). The microwear results for both palaeopopulations are as well typical for species that incorporate fruit and seeds in their diet and point to *M. flourensianus* as a fruit/seed browser. As mentioned, only some individuals show very few large pits and lack puncture-like pits, and have results more typical of leaf browsing, which can result from dietary variation intraspecifically or interseasonally.

The second moschid taxon in Steinheim a. A., *M.*? *eiselei*, does not show a strong signal for a fruit enriched diet. The mesowear pattern in the young *M.*? *eiselei* individuals is more similar to modern browsers, with whom it also clusters in the analysis. This indicates that this taxon was less frugivorous than *M. flourensianus*. The two old individuals of *M.*? *eiselei* appear to be leaf browsers as well based on their microwear. As sample size is low and as older individuals may shift their normal dietary patterns due to a wearing down of cusp morphology, we are aware that the results remain tentative. However, both, mesowear and microwear, delivered a stronger leaf browsing signal in *M.*? *eiselei* than in *M. flourensianus*. And, even though data are few so far, these differences in micro- and mesowear between *M. flourensianus* and *M.*? *eiselei* could indeed result from niche partitioning among the two sympatric moschids.

Frugivory in fossil moschids was reconstructed in several late Miocene localities by micro- and mesowear as well as isotopic measurements: Merceron (2009) described *Micromeryx flourensianus* from Atzelsdorf (late Miocene; Austria) as a browser enriching its diet by fruit. Merceron *et al.* (2007) classified *Micromeryx* from Rudabánya (late Miocene, Hungary) as a fruit browser based on microwear and as an intermediate feeder based on mesowear, explaining the difference as a possible signal of seasonality in diet preferences or food availability. Isotopic measurements for the locality revealed relatively low values in $\delta^{13}C$ in this taxon in comparison to the whole fauna from Rudabánya (Eastham *et al.* 2016), also indicating that the long-term signal could be more influenced by subcanopy browsing rather than intensive frugivory.

During the middle Miocene, frugivory could still have played a major role for moschids in Western and Central Europe. Besides the here presented data the first isotopic measurements on moschid enamel from middle Miocene localities (i.e., *Micromeryx flourensianus* from Steinheim a. A. and from the locality Gratkorn (late middle Miocene, Austria)) indicate a fruit enriched diet as well (Tütken *et al.* 2006; Aiglstorfer *et al.* 2014a). So far, only a few specimens have been measured for only two localities (Steinheim a. A.: n=2; Gratkorn: n=1) and thus allow only a tentative interpretation. However, the relatively high $\delta^{13}C$ values (Tütken *et al.* 2006; Aiglstorfer *et al.* 2014a) may result from considerable fruit consumption (see Cerling *et al.* [2004] and Codron *et al.* [2005] for modern data on ^{13}C enrichment in fruits and frugivores).

Diet of Modern Moschidae

Fruits and seeds play an important role in the diet of many modern ungulates. Frugivory as main dietary trait can be observed in ungulates with small body sizes (Bodmer 1989; Clauss *et al.* 2013).The small bovid *Cephalophus* possesses a diet consisting of 71% fruit on average or more (Gagnon & Chew 2000). It inhabits areas that provide a high availability of fruits during most of the year, like tropical forests or rain forests (Castelló 2016). But fruits and nuts can also represent a seasonal fall-back resource, when preferred food items are less available (Ramdarshan *et al.* 2016). Merceron *et al.* (2004) described acorn as a significant part of the diet in a french population of *Capreolus capreolus* (Linnaeus, 1758) during autumn and winter, when other resources were low.

Modern moschids mostly live in cold climate environments and although small in body size do not show a pronounced degree of frugivory (Green 1986; Green & Kattel 1997; Groves 2011; Pan *et al.* 2015). Groves (2011) described modern moschids as concentrate selectors that eat high-protein, high-calorie, low-fiber plants, comprising mainly moss and lichens in winter, enriched by buds and shoots in spring, and consisting of mainly broadleaved grasses and bracken

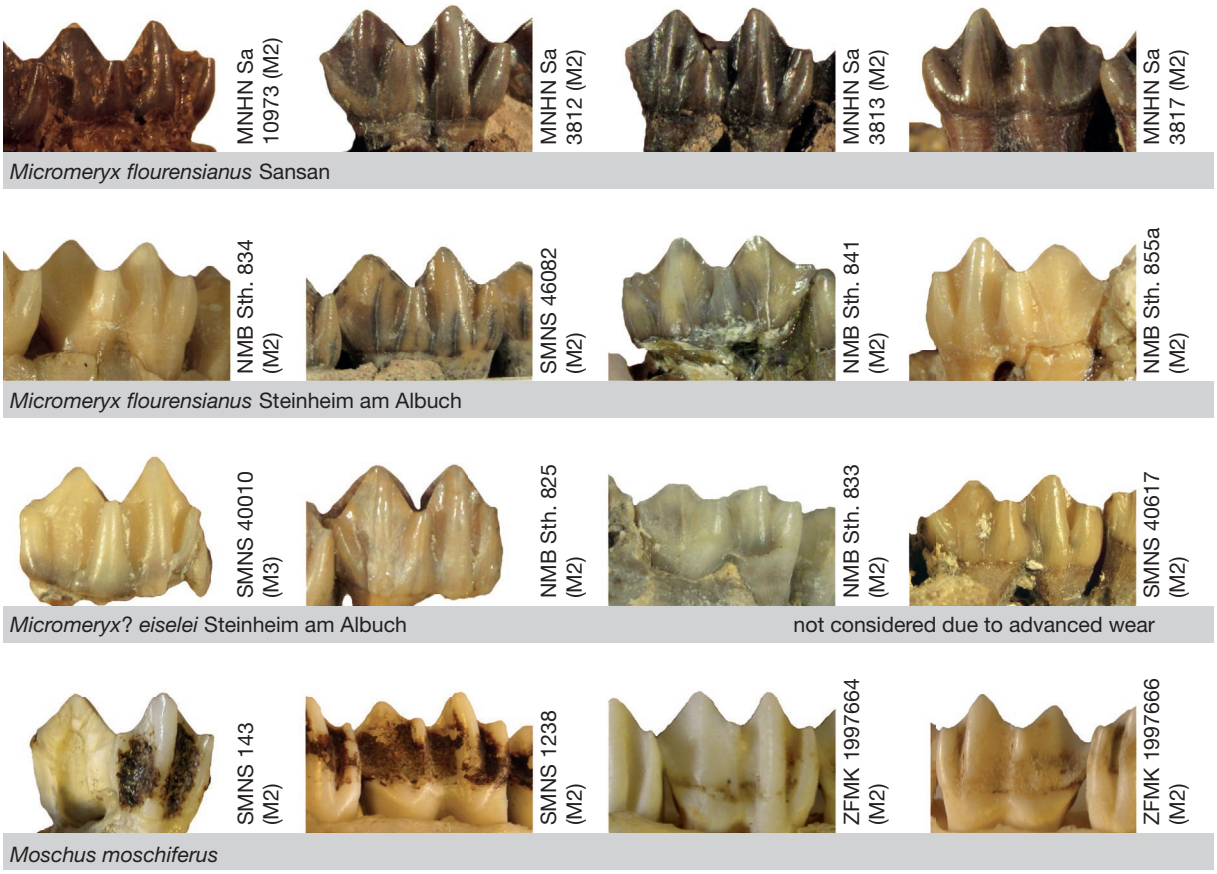

Fig. 3. — Labial walls of upper molars in *Micromeryx flourensianus* Lartet, 1851 from Sansan and Steinheim am Albuch, *Micromeryx*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017, and *Moschus moschiferus* Linnaeus, 1758 to show differences of mesowear (specimens not to scale).

in summer. Animal matter as part of the diet seems to be rather rare (Domanov 2013). The only moschids explicitly cited as living in evergreen forests are *Moschus chrysogaster* and *M. leucogaster* (Green 1986; Green & Kattel 1997; Groves 2011). A considerable nut input in the diet was mentioned only for *Moschus chrysogaster* by Zhixiao & Helin (2002) in terms of seasonal feeding on acorns (90 % of the ruminal content in populations living in oak forests), and for the region around Irkutsk (Russia), where Heptner *et al.* (1967) noted that moschids include pine nuts in their diet. Green (1987) found high proportions (varying seasonally) of leaves (forbs and woody leaves) and lichens in the diet of *M. chrysogaster* in a study on feces in North India. For *M. moschiferus*, lichens, especially arboreal lichens, are a significant part of its diet (Bannikov *et al.* 1978; Domanov 2013; Zaitsev *et al.* 2015). Groves (2011) stated that stomach contents of *M. moschiferus* revealed even 70% lichens in winter, and 50% in summer, which is higher than known for any other ruminant. Prikhod'ko (2015) corroborated that lichens comprise a considerable part of the modern moschid diet, although variable in its extent in the different populations. The author stated that the supposed frugivory for modern moschids often found in literature might indeed represent a regional signal of one population of the southern part of the genus' range, which fits with the observations on populations of *Moschus chrysogaster* mentioned above. Sridhara *et al.* (2016) stated as well that they could not find any references for modern moschids as seed dispersers in their summary on frugivory and seed dispersal by large herbivores in Asia.

Our data for four modern *Moschus* individuals from the collections in Stuttgart and Bonn fit well to the observations that fruit/seed consumption is not predominant in moschids today. Although the mesowear pattern is similar to frugivorous taxa, the microwear pattern in three individuals is more typical of browsing with a certain amount of bark or twig consumption and does not indicate fruit consumption. Especially the total lack of puncture pits (typical for fruit/seed browsers) in these three specimens differs distinctly from the signal of frugivores. As mentioned, only one specimen of *Moschus moschiferus* possesses puncture-like pits and mixed scratches in the microwear, which, in combination with the position in the morphospace (Fig. 6), indicates likely fruit browsing. For the other specimens lichen consumption might explain both, meso- and microwear. Feeding on lichens often results in incorporation of bark and twigs and can produce a mesowear signal indicating harder diet, but a microwear without the puncture-like pits that are typical for frugivores. Furthermore lichenophagy produces microwear patterns characterized by high numbers of pits, low scratch/pit ratios, and a high number of gouges (Rivals & Semprebon 2017),

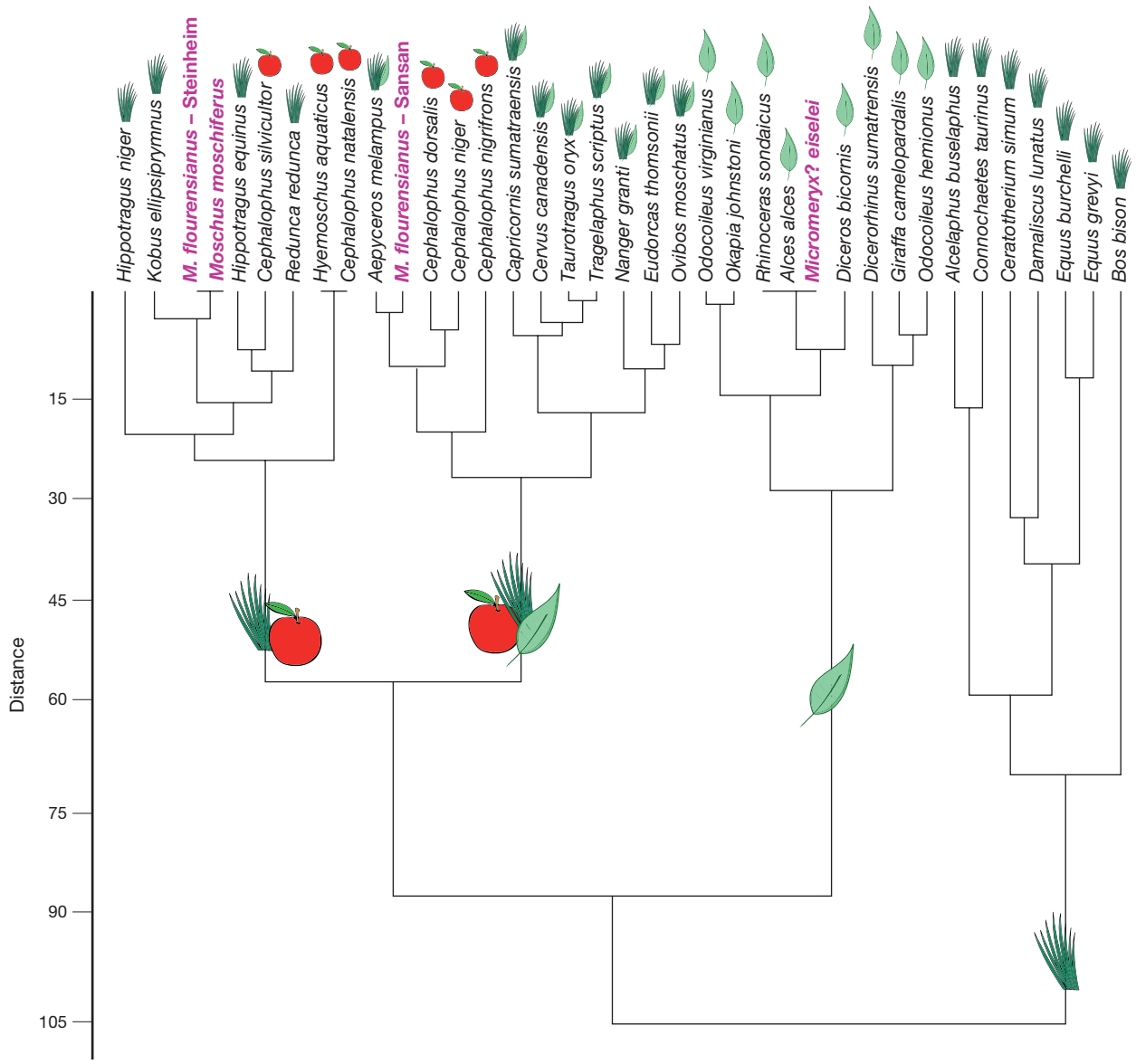

FIG. 4. — Cluster analysis for *Micromeryx* Lartet, 1851 from Sansan and Steinheim am Albuch and modern *Moschus moschiferus* Linnaeus, 1758 in comparison to modern taxa based on the variables "%sharp", "%rounded", "%blunt", "%high relief". Symbols and colors: **Bold fonts**, *M. flourensianus* Lartet, 1851 from Sansan and Steinheim a. A., *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017, and *Moschus moschiferus*; **Normal fonts**, modern comparison taxa; , extant grazers; , extant frugivores; , extant leaf browsers; , extant mixed feeders.

which fits well to the pattern we observed in our *Moschus* sample (Figs 6, 7A). The coarse and hypercoarse scratches (Fig. 7B) we found in the modern *Moschus* sample point to processing of hard objects as well (e.g. bark or twigs), which might be also a side effect of feeding on arboreal lichen, as mentioned above.

DIET OF MOSCHIDAE: FROM THE PAST TO THE PRESENT

Thus far, we did not find any indication for a considerable lichen consumption in fossil Moschidae. However, as the fossil record of lichens is very scarce (see e.g. Honegger *et al.* [2013]), it is not easy to generally estimate their role as a food resource in palaeoecosystems. We have to take into account that our view on lichen distribution is strongly biased by today's direct and indirect anthropogenic impact on ecosystems all over the world. Widespread air pollution as well as habitat destruction and fragmentation has led to much altered distribution patterns for lichens in modern ecosystems compared to pre-industrial conditions (Wirth 1995; Ellis *et al.* 2011). From what we know on climate and environmental conditions in Central and Western Europe during the middle Miocene, and especially for the here studied localities (see discussion below for more details), we can assume that lichens were also present in these ecosystems, considering the distribution pattern of lichens in modern ecosystems, (e.g. from regions with a Mediterranean climate in Italy [Nimis & Tretiach 1995; Zedda 2002; Thüs & Licht 2006]). However, taking into consideration that climate

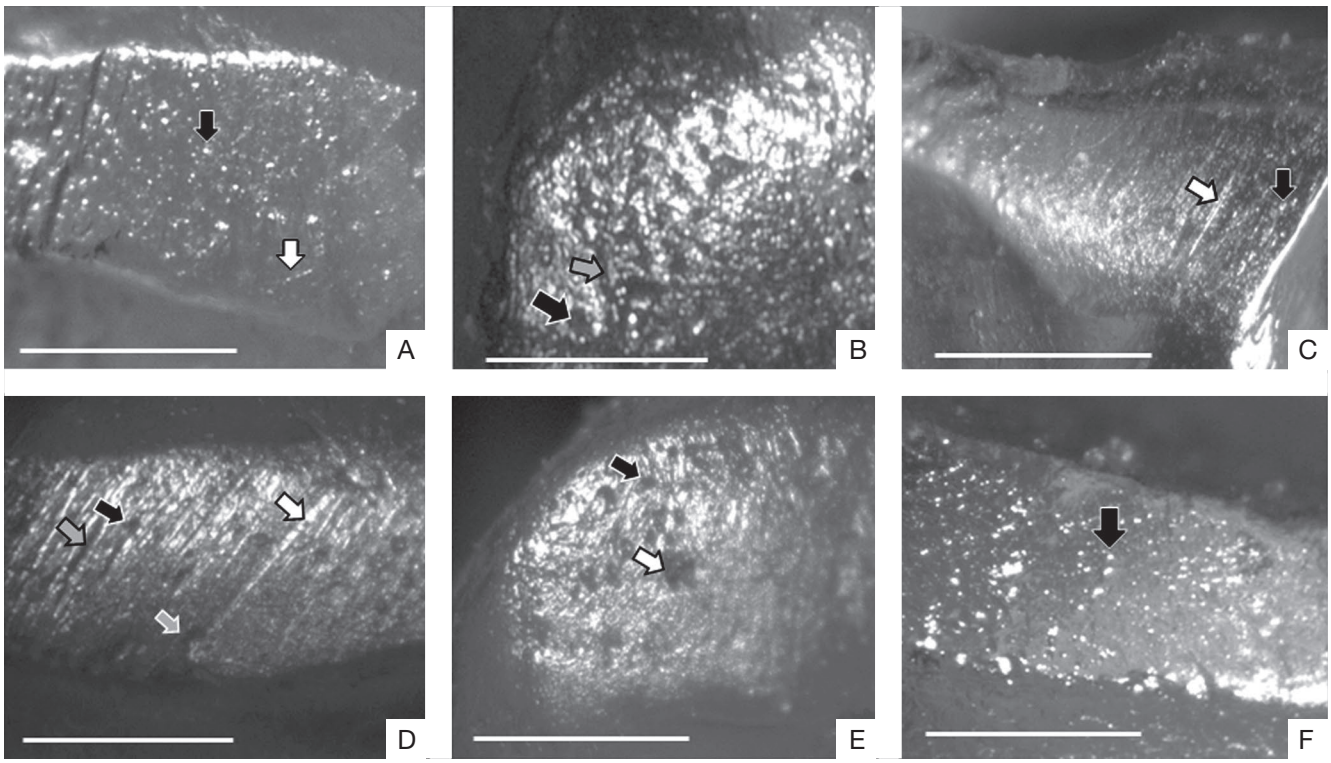

Fig. 5. — Selected microwear features: **A**, *Micromeryx flourensianus* Lartet, 1851 (MNHN.F.SA3813) from Sansan, leaf browsing phase (↗, small pit; ⇗, fine scratch); **B**, *Micromeryx flourensianus* (MNHN.F.SA3817) from Sansan, fruit browsing phase (↗, puncture-like large pit; ↗, hypercoarse scratch); **C**, *Micromeryx*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 (NMB Sth. 833) from Steinheim am Albuch, leaf browsing phase (↗, small pit; ⇗, fine scratch); **D**, *Micromeryx flourensianus* (NMB Sth. 836) from Steinheim am Albuch, fruit browsing phase (↗, puncture-like large pit; ⇗, coarse scratch; ↗, gouge; ↗, hypercoarse scratch); **E**, *Moschus moschiferus* Linnaeus, 1758 (SMNS 143), fruit browsing phase (↗, puncture-like large pit; ⇗, gouge); **F**, *Moschus moschiferus* (ZFMK 1997.664) (↗, small pit). Scale bars: 0.4 mm. All photos were taken at 50×.

conditions (no indications for temperatures below zero, nor for snow cover, or a pronounced dry season) still allowed a sufficient supply of nutrient richer diets all year round, lichens were assumedly less relevant in the diet of Miocene herbivores from this realm, as lichens often comprise mainly a fall-back resource during winter (Grueter *et al.* 2009; Xiang *et al.* 2012; Zhao *et al.* 2015; Ecke *et al.* 2018) (information on lichens: pers. comm. H. Thüs, 05.09.2018).

Comparing the diets of fossil and modern Moschidae, a generally wider dietary plasticity is indicated for their evolutionary history than we would expect based on the modern record only. This could possibly represent a shift from a facultative frugivorous browser to lichenophagy as proposed by Prikhod'ko (2015) at the turn of the Pliocene to the Pleistocene. Pan *et al.* (2015) think that the common ancestor of modern Moschidae lived on the margin of the Tibet Plateau or the adjacent mountains. Thus, a diet including a considerable amount of fruit could have been very likely for this ancestor. This might still be traceable in the possibly most ancient *Moschus* clade, including *M. chrysogaster*, still inhabitating evergreen oak forests today. Actually, *M. chrysogaster* has been named as the most basal modern moschid, although there remains some controversy about this issue (Su *et al.* 1999, 2001; Zhang *et al.* 2004; Agnarsson & May-Collado 2008; Vislobokova & Lavrov 2009).

To understand how, when, and to what extent a dietary shift occurred during the evolution of Moschidae, more studies will be needed; also taking into account that lichenophagy shows similar trends as frugivory in the isotopic signal of enamel (Drucker *et al.* 2012) and that the microwear pattern for different types of lichen is still unresolved (Rivals & Semprebon 2017).

Sansan and Steinheim am Albuch: Moschids and Environment

Another aim of our study was an intraspecific comparison of the ecology in *Micromeryx flourensianus* between the assemblages from Sansan and Steinheim a. A. Therefore, we evaluated our results in light of other environmental data available for the localities.

The Sansan locality was considered one of the last sites still representing the humid and warm conditions of the Miocene Climatic Optimum in Western Europe and is the youngest proof of crocodiles naturally occurring in France (Ginsburg & Bulot 1997; Antunes 2000). However, with only five teeth assigned to *Diplocynodon* cf. *styriacus* Hofmann, 1885 by Antunes (2000), the crocodile record is quite scarce and indicates already a strong decline during that time. Furthermore, the reference to Sansan is just by a label "Crocodile, Sansan, 1981", which means that the provenience of this reptile from the mammal bearing horizons is rather ambiguous. Costeur

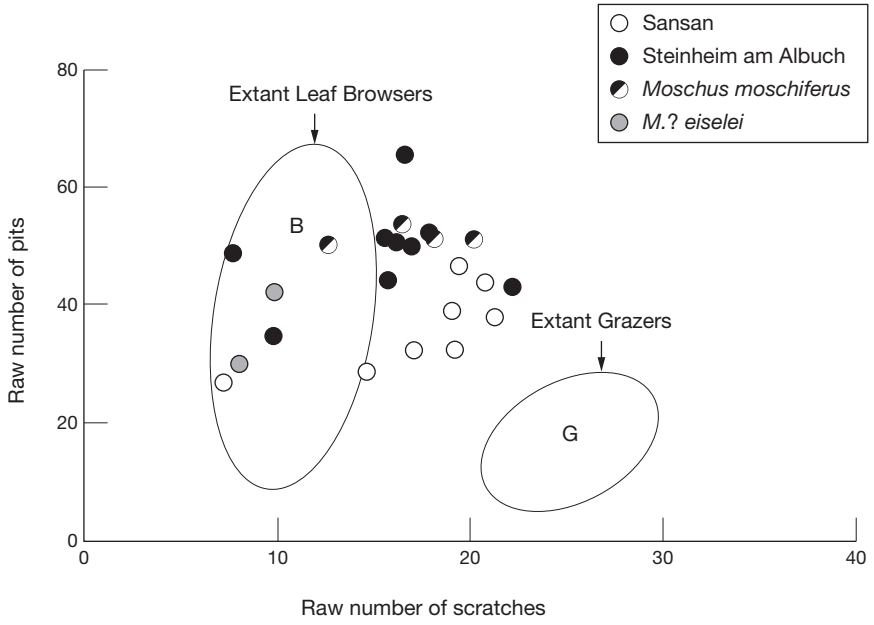

Fig. 6. — Bivariate plot with raw number of scratches versus raw number of pits in *Micromeryx flourensianus* Lartet, 1851 from Sansan (○) and Steinheim am Albuch (●), in *M.*? *eiselei* Aiglstorfer, Costeur, Mennecart & Heizmann, 2017 (◍), and in *Moschus moschiferus* Linnaeus, 1758 (◩) plotted in reference to extant leaf dominated ungulate browsers (**B**), and extant grazers (**G**) at 35 times magnification (extant comparative data from Semprebon 2002 and Solounias & Semprebon 2002). Gaussian confidence ellipses (p = 0.95) on the centroid are indicated for the extant leaf browsers and grazers (convex hulls) adjusted by sample size.

et al. (2012) reconstructed a forested habitat in a subtropical to tropical context for the Sansan locality. Furthermore, they stated that the environment must have also shown more open areas and swamps and suggested an MAT of about 16° to 19°C (with a winter temperature of 7°C and the highest temperature of more than 25°C) and a marked seasonality. Although Costeur *et al.* (2012) think of Sansan as a locality still typical for the Miocene Climatic Optimum, they observe first indications for a climate change in its mammal assemblage. Macroflora as well as palynoflora comprise mainly wet habitat elements and unfortunately do not allow any assumptions on climate and vegetation in general (pers. comm. J. Eder, 14.06.2018). Solounias & Moelleken (1994) found a browsing signal in the early bovid *Eotragus* Pilgrim, 1939 and a mixed feeding signal in the early cervid *Dicrocerus* Lartet, 1837 from Sansan, which they considered well in accordance with a woodland habitat. As smallest ruminant in the locality the dietary adaptation of *Micromeryx flourensianus* as a frugivore browser fits very well in the environment of Sansan. Even though the record for the macroflora in Sansan is not very rich, with *Celtis lacunosa* (Reuss) Kirch. and *Myristicarpum miocenicum* Gregor (Blanc-Louvel 2000) there is a record of plants providing fruits suitable for a ruminant diet. The mostly frugivorous *Cephalophus callipygus* Peters, 1876 and *C. dorsalis* Gray, 1846 are known to feed on *Staudtia gabonensis* Warb., a modern member of the Myristicaceae (Feer 1989).

Based on the floral content in Steinheim a. A. Kovar-Eder & Schweigert (2018) reconstructed the climate for this locality as warm-temperate with cooler and/or drier conditions compared to previous periods, and seasonal fluctuations in humidity. They described the vegetation as subhumid sclerophyllous to broad-leaved deciduous forest type. In Kovar-Eder & Teodiris (2018) Steinheim a. A. clusters with the "*Quercus*" communities of subhumid sclerophyllous forests from the Meili Snow Mountains (Yunnan, China). The composition of the land snail fauna from Steinheim a. A. indicates warmer and drier micro-habitats than in the stratigraphically older *silvana*-beds (Höltke & Rasser 2017). Based on ectothermic vertebrates, Böhme *et al.* (2011) reconstructed a MAP of 706 mm for Steinheim a. A. during the lake sedimentation (174 mm less than what they found today for Heidenheim [10 km E of Steinheim a. A., also located on the karstic plateau of the Swabian Alb]). Tütken *et al.* (2006) reconstructed warm-temperate climatic conditions, possibly with a high humidity for the area around the site Steinheim a. A. However, due to significant enrichment in ^{18}O of the lake water, they still assume considerable evaporation for the long-term freshwater lake (Tütken *et al.* 2006). The mammal community, more or less originating from exactly the same layers as the moschid remains (Heizmann & Reiff 2002; R. Ziegler pers. comm., 09.2018), indicates the presence of closed environments (predominantly browsing taxa dwelling mostly in closed environments like e.g. cervids, '*Palaeomeryx*' *eminens* von Meyer, 1847, and *Brachypotherium brachypus* (Lartet, 1837) [Köhler 1993; Tütken *et al.* 2006; Tütken & Vennemann 2009; Merceron *et al.* 2012; Aiglstorfer *et al.* 2014a]; small mammals categorized as "forest specialists" such as *Muscardinus* Kaup, 1829 and *Eumyarion* Thaler, 1966 in Blanco *et al.* [2018]) and open environments (mixed feeders like *Gomphotherium steinheimense* (Klähn, 1922), *Lartetotherium sansaniense* (Lartet *in* Laurillard, 1848) for large mammals [Tütken *et al.* 2006; Tütken & Vennemann 2009; Aiglstorfer *et al.* 2014a]; small mammals more common in open environments like Ochotonidae [Hordijk 2010]). The most diverse terrestrial plants

in Steinheim a. A. are oaks (*Quercus drymeja* Unger, *Q.*? *gigas* Göppert emend. Walther & Zastawniak, *Q. kubinyii* (Kováts ex Ettingsh.) Czeczott, *Q. mediterranea* Unger, *Q. pseudocastanea* Goeppert), and well documented are *Celtis japeti* Unger, *C. lacunosa*, *Podocarpium podocarpum* (A. Braun) Herendeen, *Populus balsamoides* Goeppert, *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba, and Sapindales leaflets of compound leaves (Kovar-Eder & Schweigert 2018). Sapindales, *Podocarpium* A. Braun *ex* Stizenberger and *Celtis* Linnaeus may have provided a considerable amount of soft fruit for *Micromeryx flourensianus*, while high nutritious nuts could have been gained especially from *Quercus* Linnaeus. Some individuals from Steinheim a. A. might have fed (at least seasonally) on acorn, comparable to the modern roe deer from France and the population of *M. chrysogaster*, both described above. They display a mixture of coarse and hypercoarse scratches (Fig. 7B), which are seen in extant ungulates that incorporate harder fruits and seeds in their diet or more twigs and bark (Solounias & Semprebon 2002).

Combining the different proxies from flora, invertebrates, ectothermic vertebrates, and mammals, with our data we can assume for the wider area around both localities, Sansan and Steinheim a. A., a mosaic environment with a marked seasonality, and, at least for Steinheim a. A., our data indicate that there was a considerable amount of folivore dietary items available in terms of arboreal leaves or maybe just scrubs in the vicinity of the lake. Combining our data from Sansan with the results of Solounias & Moelleken (1994) for other ruminant taxa, enough biomass was apparently available for a folivore-based diet for several ruminants in Sansan as well. Due to the stronger influence of the "Miocene Climatic Event" and/or the position on the karstic environment of the Swabian Alb, the conditions in Steinheim a. A. were already more arid and/or comprised a stronger seasonality than in Sansan. This fits as well to our data as *Micromeryx flourensianus* individuals from Steinheim a. A. have more pits overall and more large pits and gouges than those from Sansan (Table 2; Fig. 7A) which is often found in ungulates that live in more open environments (Solounias & Semprebon 2002). Surprisingly Steinheim a. A. has more individuals with scratch numbers in or closer to the leaf browsing range (Fig. 6) which seems to indicate more leaf-browsing in the individuals from Steinheim a. A. than in those from Sansan. This is corroborated as well by the fact that the second moschid taxon in Steinheim a. A., *M.*? *eiselei*, shows a more distinct browsing signal. However, a higher degree of browsing does not contradict more open landscapes, considering that the modern *Antilocapra americana* (Ord, 1815), living in the open landscape of the North American prairies has a dental wear signal typical for a browser (Semprebon & Rivals 2007), as it feeds extensively on the sagebrush *Artemisia tridentata* Nutt. and less on grass.

The environmental data from Sansan and Steinheim a. A., including the reconstructed moschid diet, show that, although Steinheim a. A. offers indications for more arid conditions, differences between the localities are smaller than expected, meaning that the environment in Sansan was most likely

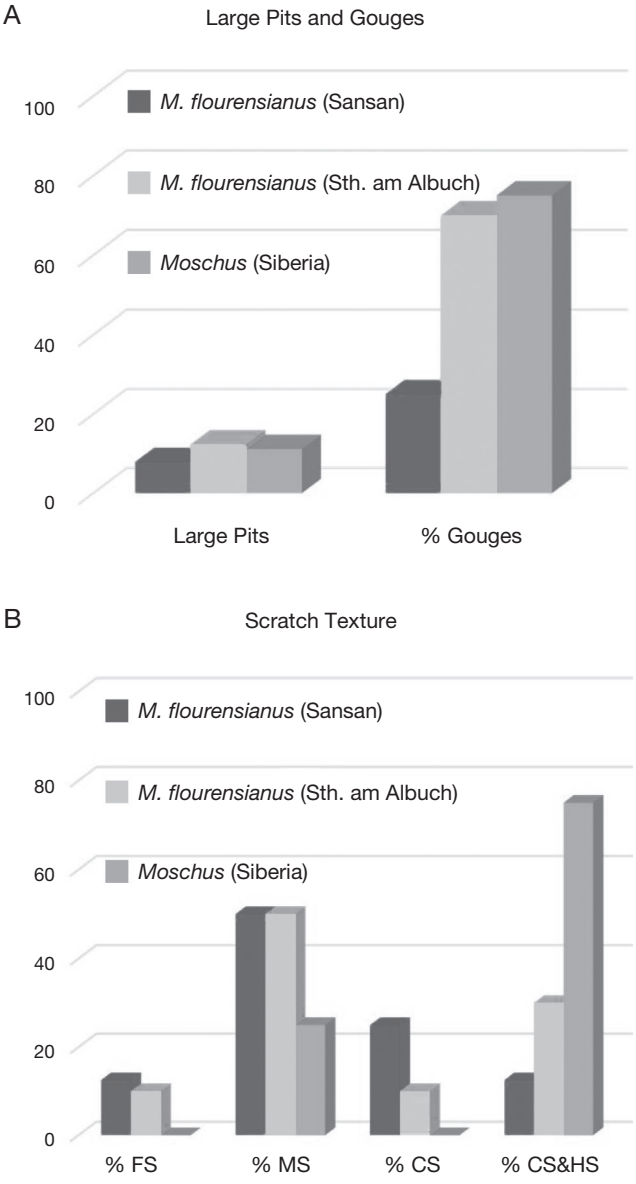

Fig. 7. — **A**, Percentage of individuals with large pits and gouges for *Micromeryx flourensianus* Lartet, 1851 from Sansan and Steinheim am Albuch (Sth. a. A.), as well as for modern *Moschus* Linnaeus, 1758 from Siberia; **B**, percentage of individuals with different scratch textures for *Micromeryx flourensianus* from Sansan and Steinheim am Albuch (Sth. a. A.), as well as for modern *Moschus* from Siberia. Abbreviations: **%FS**, percentage of individuals with fine scratches; **%MS**, percentage of individuals with mixed scratches; **%CS**, percentage of individuals with coarse scratches; **%C&HC**, percentage of individuals with coarse and hypercoarse scratches.

also quite different from the conditions during the "high times" of the Miocene Climatic Optimum, but more similar to Steinheim a. A. We think that Sansan was indeed already affected by the "Miocene Climatic Event" as indicated also by Costeur *et al.* (2012). Sansan marks the onset of the wide moschid dispersal in Europe. And we consider this dispersal as strongly linked to the change in the climatic conditions and that *Micromeryx* might actually prove an index-taxon for a climate change to stronger aridity/seasonality, which is corroborated also by the fact that Steinheim a. A. represents the so far richest accumulation of fossil moschids.

CONCLUSION

Our data on micro- and mesowear in *Micromeryx flourensianus* from Sansan and Steinheim a. A. in combination with the reconstructed climates and environments, show that fruits were an essential, but not exclusive part of the diet of *M. flourensianus* in both localities. This corroborates other studies on a frugivorous diet of Miocene Moschidae and with the record from Sansan provides the so far oldest evidence for fruit consumption in the family.

The second moschid in Steinheim a. A., *M.*? *eiselei*, had a stronger leaf browsing signal, which indicates ecologic niche partitioning for the two sympatric moschid species from Steinheim a. A.

Combining our study with literature data (Tütken *et al.* 2006; Merceron *et al.* 2007; Merceron 2009; Aiglstorfer *et al.* 2014a; Eastham *et al.* 2016), it appears that frugivory seems to have been a common trait in moschids in Miocene ecosystems, with a possibly decreasing trend from middle to late Miocene. This reveals a different diet in the early moschids than it is usually the case in the modern genus, *Moschus*, whose diet comprises less fruits, but a considerable amount of lichens.

A comparison between the palaeopopulations from Sansan and Steinheim a. A. revealed that, though the record from Steinheim a. A. points to more arid conditions, the environment could have been more alike in both localities than expected. This corroborates the assumption that the Sansan Palaeoecosystem was already affected by the effects of the "Miocene Climatic Event". Taking into account the stratigraphic distribution of European moschids the wide dispersal of the family in Europe might actually be linked to this event, and, as mentioned above, *Micromeryx* might indeed prove very helpful in tracking the middle Miocene climate change.

Acknowledgements
We want to thank M. Boller for help with casts, C. Argot (MNHN), L. Costeur (NMB), R. Ziegler (SMNS), E. Bärmann (ZFMK), S. Merker (SMNS), and C. Zeitler (SMNS) for loans and for the permission to take casts for microwear. J. Eder, P. Havlik, E. Heizmann, C. Krause, M. Rasser, G. Schweigert, H. Thüs, and R. Ziegler are thanked for discussions. We want to thank the Gesellschaft zur Förderung des Naturkundemuseums Stuttgart e.V. for financial support and the reviewers, B. Mennecart and L. Costeur for their great help in improving the manuscript.

REFERENCES

Agnarsson I. & May-Collado L. J. 2008. — The phylogeny of Cetartiodactyla: The importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species-level phylogenies. *Molecular Phylogenetics and Evolution* 48: 964-985. https://doi.org/10.1016/j.ympev.2008.05.046

Aiglstorfer M. & Costeur L. 2013. — The Moschidae of Dorn-Dürkheim 1 (Germany). *Palaeobiodiversity and Palaeoenvironments* 93: 207-215. https://doi.org/10.1007/s12549-013-0117-9

Aiglstorfer M., Bocherens H. & Böhme M. 2014a — Large mammal ecology in the late Middle Miocene Gratkorn locality (Austria). *Palaeobiodiversity and Palaeoenvironments* 94: 189-213. https://doi.org/10.1007/s12549-013-0145-5

Aiglstorfer M., Rössner G. E. & Böhme M. 2014b — *Dorcatherium naui* and pecoran ruminants from the late Middle Miocene Gratkorn locality (Austria). *Palaeobiodiversity and Palaeoenvironments* 94: 83-123. https://doi.org/10.1007/s12549-013-0141-9

Aiglstorfer M., Costeur L., Mennecart B. & Heizmann E. P. J. 2017. — *Micromeryx*? *eiselei* – A new moschid species from Steinheim am Albuch, Germany, and the first comprehensive description of moschid cranial material from the Miocene of Central Europe. *PLOS ONE* 12: e0185679. https://doi.org/10.1371/journal.pone.0185679

Aiglstorfer M., Mayda S. & Heizmann E. P. J. 2018. — First record of late middle Miocene Moschidae from Turkey: *Micromeryx* and *Hispanomeryx* from Catakbağyaka (Muğla, SW Turkey). *Comptes Rendus Palevol* 17: 178-188. https://doi.org/10.1016/j.crpv.2017.10.001

Aiglstorfer M., Peigné S. & Heizmann E. P. J. 2019. — Who killed *Micromeryx flourensianus*? Predation on ruminants from the Middle Miocene of France and taphonomic considerations. *Lethaia*. https://doi.org/10.1111/let.12322

Antunes M. T. 2000. — Les Crocodiliens de Sansan, *in* Ginsburg L. (ed), *La Faune miocène de Sansan et son environment*. Muséum national d'Histoire naturelle, Paris: 315-319 (Mémoires du Muséum national d'Histoire naturelle; 183).

Bannikov A. G., Ustinov S. K. & Lobanov P. N. 1978. — The Musk deer *Moschus moschiferus* in USSR, *in* IUCN monograph: 1-51.

Bärmann E. V. & Rössner G. E. 2011. — Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mammalian Biology – Zeitschrift für Säugetierkunde* 76 (6): 762-768. https://doi.org/10.1016/j.mambio.2011.07.002

Bibi F. 2013. — A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evolutionary Biology* 13: 1-15. https://doi.org/10.1186/1471-2148-13-166

Bibi F. 2014. — Assembling the ruminant tree: combining morphology, molecules, extant taxa, and fossils. *Zitteliana* 32: 197-211. https://doi.org/10.5282/ubm/epub.22396

Blanc-Louvel C. 2000. — La macroflore de Sansan, *in* Ginsburg L. (ed.), *La Faune miocène de Sansan et son environment*. Muséum national d'Histoire naturelle, Paris: 109-116 (Mémoires du Muséum national d'Histoire naturelle; 183).

Blanco F., Gómez Cano A. R., Cantalapiedra J. L., Domingo M. S., Domingo L., Menéndez I., Flynn L. J. & Hernández Fernández M. 2018. — Differential responses of Miocene rodent metacommunities to global climatic changes were mediated by environmental context. *Scientific Reports* 8: 2502. https://doi.org/10.1038/s41598-018-20900-5

Bodmer R. E. 1989. — Frugivory in Amazonian Artiodactyla: evidence for the evolution of the ruminant stomach. *Journal of Zoology* 219: 457-467. https://doi.org/10.1111/j.1469-7998.1989.tb02593.x

Böhme M., Winklhofer M. & Ilg A. 2011. — Miocene precipitation in Europe: Temporal trends and spatial gradients. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304: 212-218. https://doi.org/10.1016/j.palaeo.2010.09.028

Buchner E., Schmieder M., Schwarz W. H. & Trieloff M. 2013. — Das Alter des Meteoritenkraters Nördlinger Ries - eine Übersicht und kurze Diskussion der neueren Datierungen des Riesimpakts. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 164: 433-445. https://doi.org/10.1127/1860-1804/2013/0037

Castelló J. R. 2016. — *Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and Relatives (Princeton Field Guides)*. Princeton University Press, Princeton, 664 p.

Cerling T. E., Hart J. A. & Hart T. B. 2004. — Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5-12. https://doi.org/10.1007/s00442-003-1375-4

Clauss M., Steuer P., Müller D. W. H., Codron D. & Hummel J. 2013. — Herbivory and Body Size: Allometries of Diet Quality and Gastrointestinal Physiology, and Implications for Herbivore Ecology and Dinosaur Gigantism. *PLOS ONE* 8: e68714. https://doi.org/10.1371/journal.pone.0068714

Codron J., Codron D., Lee-Thorp J. A., Sponheimer M. & De Ruiter D. 2005. — Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research* 35: 43-52. https://hdl.handle.net/10520/EJC117206

Costeur L., Guérin C. & Maridet O. 2012. — Paléoécologie et paléoenvironnement du site miocène de Sansan, *in* Peigné S. & Sen S. (eds), *Mammifères de Sansan*. Muséum national d'Histoire naturelle, Paris: 661-693 (Mémoires du Muséum national d'Histoire naturelle ; 203).

Damuth J. 1990. — Problems in estimating body masses of archaic ungulates using dental measurements, *in* Damuth J. & MacFadden B. (eds), *Body Size in Mammalian Paleobiology Estimations and Biological Implications*. Cambridge University Press, Cambridge: 229-254.

Domanov T. A. 2013. — Musk deer *Moschus moschiferus* nutrition in the Tukuringra Mountain Range, Russian Far East, during the snow season. *Russian Journal of Theriology* 12: 91-97. https://doi.org/10.15298/rusjtheriol.12.2.05

Dos Reis M., Inoue J., Hasegawa M., Asher R. J., Donoghue P. C. J. & Yang Z. 2012. — Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proceedings of the Royal Society of London B: Biological Sciences* 279: 3491-3500. https://doi.org/10.1098/rspb.2012.0683

Drucker D. G., Hobson K. A., Münzel S. C. & Pike-Tay A. 2012. — Intra-individual variation in stable carbon (δ13C) and nitrogen (δ15N) isotopes in mandibles of modern caribou of Qamanirjuaq (*Rangifer tarandus groenlandicus*) and Banks Island (*Rangifer tarandus pearyi*): Implications for tracing seasonal and temporal changes in diet. *International Journal of Osteoarchaeology* 22: 494-504. https://doi.org/10.1002/oa.1220

Eastham L. C., Feranec R. S. & Begun D. R. 2016. — Stable isotopes show resource partitioning among the early Late Miocene herbivore community at Rudabánya II: Paleoenvironmental implications for the hominoid, *Rudapithecus hungaricus*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 454: 161-174. https://doi.org/10.1016/j.palaeo.2016.04.036

Ecke F., Berglund Å. M. M., Rodushkin I., Engström E., Pallavicini N., Sörlin D., Nyholm E. & Hörnfeldt B. 2018. — Seasonal shift of diet in bank voles explains trophic fate of anthropogenic osmium? *Science of The Total Environment* 624: 1634-1639. https://doi.org/10.1016/j.scitotenv.2017.10.056

Ellis C. J., Yahr R. & Coppins B. J. 2011. — Archaeobotanical evidence for a massive loss of epiphyte species richness during industrialization in southern England. *Proceedings of the Royal Society B: Biological Sciences* 278 (1724): 3482-3489. https://doi.org/10.1098/rspb.2011.0063

Feer F. 1989. — Comparaison des régimes alimentaires de *Cephalophus callipygus* et *C. dorsalis*, bovidés sympatriques de la forêt sempervirente africaine. *Mammalia* 53: 563-604. https://doi.org/10.1515/mamm.1989.53.4.563

Fortelius M. & Solounias N. 2000. — Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301: 1-36. https://doi.org/10.1206/0003-0082(2000)301<0001:FCOUMU>2.0.CO;2

Gagnon M. & Chew A. E. 2000. — Dietary Preferences in Extant African Bovidae. *Journal of Mammalogy* 81: 490-511. https://doi.org/10.1644/1545-1542(2000)081<0490:DPIEAB>2.0.CO;2

Gentry A. W. 1994. — The miocene differentiation of old world Pecora (Mammalia). *Historical Biology* 7: 115-158. https://doi.org/10.1080/10292389409380449

Gentry A. W. 2000. — The ruminant radiation, *in* Vrba E. S. & Schaller G. B. (eds), *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*. Yale University Press, New Haven: 11-45.

Ginsburg I. & Bulot C. 1997. — Les *Diplocynodon* (Reptilia, Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. *Geodiversitas* 19 (1): 107-128.

Ginsburg L. & Bulot C. 2000. — Le cadre stratigraphique de site de Sansan, *in* Ginsburg L. (ed.), *La Faune miocène de Sansan et son environment*. Muséum national d'Histoire naturelle, Paris: 39-67 (Mémoires du Muséum national d'Histoire naturelle; 183).

Green M. J. B. 1986. — The Distribution, Status and Conservation of the Himalayan Musk Deer *Moschus chrysogaster*. *Biological Conservation* 35: 347-375. https://doi.org/10.1016/0006-3207(86)90094-7

Green M. J. B. 1987. — Diet Composition and Quality in Himalayan Musk Deer Based on Fecal Analysis. *The Journal of Wildlife Management* 51: 880-892. https://doi.org/10.2307/3801755

Green M. J. B. & Kattel B. 1997. — Musk deer: little understood, even its scent, *in* First International Symposium on Endangered Species Used in Traditional East Asian Medicine, Hong Kong: 1-18. https://biodiversitylibrary.org/page/38687582

Groves C. P. 2011. — Family Moschidae (musk-deer), *in* Wilson D. E. & Mittermeier R. A. (eds), *Handbook of the Mammals of the World*. Vol. 2. Lynx Edicions, Barcelona: 336-348.

Grueter C. C., Li D., Ren B., Wei F. & van Schaik C. P. 2009. — Dietary Profile of *Rhinopithecus bieti* and Its Socioecological Implications. *International Journal of Primatology* 30: 601-624. https://doi.org/10.1007/s10764-009-9363-0

Hassanin A., Delsuc F., Ropiquet A., Hammer C., Jansen van Vuuren B., Matthee C., Ruiz-Garcia M., Catzeflis F., Areskoug V., Nguyen T. T. & Couloux A. 2012. — Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* 335 (1): 32-50. https://doi.org/10.1016/j.crvi.2011.11.002

Hassanin A. & Douzery E. J. P. 2003. — Molecular and Morphological Phylogenies of Ruminantia and the Alternative Position of the Moschidae. *Systematic Biology* 52: 206-228. https://doi.org/10.1080/10635150390192726

Heizmann E. P. J. & Reiff W. 2002. — *Der Steinheimer Meteorkrater*. Verlag Dr. Friedrich Pfeil, München, 160 p.

Heptner V. G., Nasimovich A. A. & Bannikov A. G. 1967. — *Artiodactyla and Perissodactyla [English translation]*. Amerind Publishing Co. Pvt. Ltd., Baba Barkha Nath Printers, New Delhi, 1147 p.

Hernández Fernández M. & Vrba E. S. 2005. — A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews* 80: 269-302. https://doi.org/10.1017/S1464793104006670

Hilgen F. J., Lourens L. J., Van Dam J. A., Beu A. G., Boyes A. F., Cooper R. A., Krijgsman W., Ogg J. G., Piller W. E. & Wilson D. S. 2012. — Chapter 29 – The Neogene Period, *in* *The Geologic Time Scale*. Elsevier, Boston: 923-978.

Holt B. G., Lessard J.-P., Borregaard M. K., Fritz S. A., Araújo M. B., Dimitrov D., Fabre P.-H., Graham C. H., Graves G. R., Jønsson K. A., Nogués-Bravo D., Wang Z., Whittaker R. J., Fjeldså J. & Rahbek C. 2013. — An Update of Wallace's Zoogeographic Regions of the World. *Science* 339: 74-78. https://doi.org/10.1126/science.1228282

Höltke O. & Rasser M. W. 2017. — Land snails from the Miocene Steinheim impact crater lake sediments (Baden-Württemberg, South Germany). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 285: 267-302. https://doi.org/10.1127/njgpa/2017/0681

Honegger R., Edwards D. & Axe L. 2013. — The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. *New Phytologist* 197: 264-275. https://doi.org/10.1111/nph.12009

HORDIJK K. 2010. — *Perseverance of Pikas in the Miocene Interplay of Climate and Competition in the Evolution of Spanish Ochotonidae (Lagomorpha, Mammalia)*. Utrecht University, Utrecht, 232 p.
IUCN 2018. — The IUCN Red List of Threatened Species. Version 2017-3. http://www.iucnredlist.org. Downloaded on 18 February 2018.
JANIS C. M. 1990. — Correlation of cranial and dental variables with body size in ungulates and macropodoids, *in* DAMUTH J. & MACFADDEN B. (eds), *Body Size in Mammalian Paleobiology Estimations and Biological Implications*. Cambridge University Press, Cambridge: 255-300.
JANIS C. M. & SCOTT K. M. 1987. — The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *American Museum Novitates* 2893: 1-85. http://hdl.handle.net/2246/5180
KÖHLER M. 1993. — Skeleton and Habitat of recent and fossil Ruminants. *Münchner Geowissenschaftliche Abhandlungen* 25: 87.
KOVAR-EDER J. & SCHWEIGERT G. 2018. — Revision of the plant assemblage of Steinheim am Albuch (Baden-Württemberg, Germany, reference locality of Neogene Mammal zone MN 7). *Bulletin of Geosciences* 93 (4): 419-456. https://doi.org/10.3140/bull.geosci.1695
KOVAR-EDER J. & TEODIRIS V. 2018. — The Middle Miocene Central European plant record revisited; widespread subhumid sclerophyllous forests indicated. *Fossil Imprint* 74: 115-134. https://doi.org/10.2478/if-2018-0009
MENNECART B. 2012. — The Ruminantia (Mammalia, Cetartiodactyla) from the Oligocene to the Early Miocene of Western Europe: systematics, palaeoecology and palaeobiogeography. *GeoFocus* 32: 1-263.
MENNECART B., DEMIGUEL D., BIBI F., RÖSSNER G. E., MÉTAIS G., NEENAN J. M., WANG S., SCHULZ G., MÜLLER B. & COSTEUR L. 2017. — Bony labyrinth morphology clarifies the origin and evolution of deer. *Scientific Reports* 7: 13176. https://doi.org/10.1038/s41598-017-12848-9
MENNECART B., SCHERLER L., HIARD F., BECKER D. & BERGER J.-P. 2012. — Large mammals from Rickenbach (Switzerland, reference locality MP29, Late Oligocene): biostratigraphic and palaeoenvironmental implications. *Swiss Journal of Palaeontology* 131: 161-181. https://doi.org/10.1007/s13358-011-0031-6
MENNECART B., ZOBOLI D., COSTEUR L. & PILLOLA G. L. 2018. — On the systematic position of the oldest insular ruminant *Sardomeryx oschiriensis* (Mammalia, Ruminantia) and the early evolution of the Giraffomorpha. *Journal of Systematic Palaeontology* 17 (8): 691-704. https://doi.org/10.1080/14772019.2018.1472145
MERCERON G. 2009. — The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria) 13. Dental wear patterns of herbivorous ungulates as ecological indicators. *Annalen des Naturhistorischen Museums Wien* 111A: 647-660.
MERCERON G., COSTEUR L., MARIDET O., RAMDARSHAN A. & GÖHLICH U. B. 2012. — Multi-proxy approach detects heterogeneous habitats for primates during the Miocene climatic optimum in Central Europe. *Journal of Human Evolution* 63: 150-161. https://doi.org/10.1016/j.jhevol.2012.04.006
MERCERON G., SCHULZ E., KORDOS L. & KAISER T. M. 2007. — Paleoenvironment of *Dryopithecus brancoi* at Rudabánya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. *Journal of Human Evolution* 53: 331-349. https://doi.org/10.1016/j.jhevol.2007.04.008
MERCERON G., VIRIOT L. & BLONDEL C. 2004. — Tooth microwear pattern in roe deer (*Capreolus capreolus* L.) from Chizé (Western France) and relation to food composition. *Small Ruminant Research* 53: 125-132. https://doi.org/10.1016/j.smallrumres.2003.10.002
MIHLBACHLER M. C., RIVALS F., SOLOUNIAS N. & SEMPREBON G. M. 2011. — Dietary Change and Evolution of Horses in North America. *Science* 331: 1178-1181. https://doi.org/10.1126/science.1196166
NEUBAUER T. A., HARZHAUSER M., KROH A., GEORGOPOULOU E. & MANDIC O. 2015. — A gastropod-based biogeographic scheme for the European Neogene freshwater systems. *Earth-Science Reviews* 143: 98-116. https://doi.org/10.1016/j.earscirev.2015.01.010
NIMIS P. L. & TRETIACH M. 1995. — The lichens of Italy – a phytoclimatical outline. *Cryptogamic Botany* 5: 199-208.
PAN T., WANG H., HU C., SUN Z., ZHU X., MENG T., MENG X. & ZHANG B. 2015. — Species delimitation in the genus *Moschus* (Ruminantia: Moschidae) and its high-plateau origin. *PLOS ONE* 10: e0134183. https://doi.org/10.1371/journal.pone.0134183
PLAZIAT J.-C. & BALTZER F. 2000. — Rôles respectifs de la sédimentation et de la diagenèse dans la constitution du gisement de vertébrés de Sansan, *in* GINSBURG L. (ed.), *La Faune miocène de Sansan et son environment*. Muséum national d'Histoire naturelle, Paris: 83-108 (Mémoires du Muséum national d'Histoire naturelle; 183).
PRIKHOD'KO V. I. 2015. — Cranial features and feeding types of subspecies forms of *Moschus moschiferus* L. (Moschidae, Cetartiodactyla). *Biology Bulletin* 42: 54-60. https://doi.org/10.1134/S1062359015010100
RAMDARSHAN A., BLONDEL C., BRUNETIÈRE N., FRANCISCO A., GAUTIER D., SURAULT J. & MERCERON G. 2016. — Seeds, browse, and tooth wear: a sheep perspective. *Ecology and Evolution* 6: 5559-5569. https://doi.org/10.1002/ece3.2241
RIVALS F., MIHLBACHLER M. C. & SOLOUNIAS N. 2007. — Effect of ontogenetic-age distribution in fossil and modern samples on the interpretation of ungulate paleodiets using the mesowear method. *Journal of Vertebrate Paleontology* 27: 763-767. https://doi.org/10.1671/0272-4634(2007)27[763:EOODIF]2.0.CO;2
RIVALS F. & SEMPREBON G. M. 2017. — Latitude matters: an examination of behavioural plasticity in dietary traits amongst extant and Pleistocene *Rangifer tarandus*. *Boreas* 46: 254-263. https://doi.org/10.1111/bor.12205
SÁNCHEZ I. M., CANTALAPIEDRA J. L., RÍOS M., QUIRALTE V. & MORALES J. 2015. — Systematics and Evolution of the Miocene Three-Horned Palaeomerycid Ruminants (Mammalia, Cetartiodactyla). *PLOS ONE* 10: e0143034. https://doi.org/10.1371/journal.pone.0143034
SÁNCHEZ I. M., DEMIGUEL D., QUIRALTE V. & MORALES J. 2011. — The first known Asian *Hispanomeryx* (Mammalia, Ruminantia, Moschidae). *Journal of Vertebrate Paleontology* 31: 1397-1403. https://doi.org/10.1080/02724634.2011.618155
SÁNCHEZ I. M., DOMINGO M. S. & MORALES J. 2009. — New data on the Moschidae (Mammalia, Ruminantia) from the upper Miocene of Spain (Mn 10–Mn 11). *Journal of Vertebrate Paleontology* 29: 567-575. https://doi.org/10.1671/039.029.0223
SÁNCHEZ I. M., DOMINGO M. S. & MORALES J. 2010. — The genus *Hispanomeryx* (Mammalia, Ruminantia, Moschidae) and its bearing on musk deer phylogeny and systematics. *Palaeontology* 53: 1023-1047. https://doi.org/10.1111/j.1475-4983.2010.00992.x
SÁNCHEZ I. M. & MORALES J. 2008. — *Micromeryx azanzae* sp. nov. (Ruminantia: Moschidae) from the middle-upper Miocene of Spain, and the first description of the cranium of *Micromeryx*. *Journal of Vertebrate Paleontology* 28: 873-885. https://doi.org/10.1671/0272-4634(2008)28[873:MASNRM]2.0.CO;2
SCOTT K. M. 1990. — Postcranial dimensions of ungulates as predictors of body mass, *in* DAMUTH J. & MACFADDEN B. (eds), *Body Size in Mammalian Paleobiology Estimations and Biological Implications*. Cambridge University Press, Cambridge: 301-336.
SEMPREBON G. M. 2002. — Advances in the reconstruction of extant ungulate ecomorphology with applications to fossil ungulates. University of Massachusetts, Amherst, 461 p.
SEMPREBON G. M., GODFREY L. R., SOLOUNIAS N., SUTHERLAND M. R. & JUNGERS W. L. 2004. — Can low-magnification stereomicroscopy reveal diet? *Journal of Human Evolution* 47: 115-144. https://doi.org/10.1016/j.jhevol.2004.06.004

SEMPREBON G. M. & RIVALS F. 2007. — Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to Recent Antilocapridae (Mammalia: Artiodactyla). *Palaeogeography, Palaeoclimatology, Palaeoecology* 253: 332-347. https://doi.org/10.1016/j.palaeo.2007.06.006

SEN S. & GINSBURG L. 2000. — La magnétostratigraphie du site de Sansan, *in* GINSBURG L. (ed.), *La Faune miocène de Sansan et son environment*. Muséum national d'Histoire naturelle, Paris: 69-81 (Mémoires du Muséum national d'Histoire naturelle; 183).

SOLOUNIAS N. & MOELLEKEN S. M. C. 1994. — Differences in diet between two archaic ruminant species from Sansan, France. *Historical Biology* 7: 203-220. https://doi.org/10.1080/10292389409380454

SOLOUNIAS N. & SEMPREBON G. M. 2002. — Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *American Museum Novitates* 3366: 1-49. https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2

SRIDHARA S., MCCONKEY K., PRASAD S. & CORLETT R. T. 2016. — Frugivory and Seed Dispersal by Large Herbivores of Asia, *in* AHRESTANI F. S. & SANKARAN M. (eds), *The Ecology of Large Herbivores in South and Southeast Asia*. Chapter 5. Springer, Heidelberg: 121-150. https://doi.org/10.1007/978-94-017-7570-0_5

STÖFFLER D., ARTEMIEVA N. A. & PIERAZZO E. 2002. — Modeling the Ries-Steinheim impact event and the formation of the moldavite strewn field. *Meteoritics & Planetary Science* 37 (12): 1893-1907.

SU B., WANG Y.-X., LAN H., WANG W. & ZHANG Y. 1999. — Phylogenetic Study of Complete Cytochrome b Genes in Musk Deer (Genus *Moschus*) Using Museum Samples. *Molecular Phylogenetics and Evolution* 12: 241-249. https://doi.org/10.1006/mpev.1999.0616

SU B., WANG Y.-X. & WANG Q.-S. 2001. — Mitochondrial DNA sequences imply anhui musk deer a valid species in genus *Moschus*. *Zoological Research* 22: 169-173.

THÜS H. & LICHT W. 2006. — Oceanic and hygrophytic lichens from the Gargano-Peninsula (Puglia/South-Eastern-Italy). *Herzogia* 19: 149-153.

TÜTKEN T. & VENNEMANN T. 2009. — Stable isotope ecology of Miocene large mammals from Sandelzhausen, southern Germany. *Paläontologische Zeitschrift* 83: 207-226. https://doi.org/10.1007/s12542-009-0011-y

TÜTKEN T., VENNEMANN T. W., JANZ H. & HEIZMANN E. P. J. 2006. — Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany: A reconstruction from C, O, and Sr isotopes of fossil remains. *Palaeogeography, Palaeoclimatology, Palaeoecology* 241: 457-491. https://doi.org/10.1016/j.palaeo.2006.04.007

VISLOBOKOVA I. 2007. — New Data on Late Miocene Mammals of Kohfidisch, Austria. *Paleontological Journal* 41: 451-460. https://doi.org/10.1134/S0031030107040119

VISLOBOKOVA I. A. 1990. — The basic features of historical development and classification of the Ruminantia. *Paleontological Journal* 24: 1-11.

VISLOBOKOVA I. A. & LAVROV A. V. 2009. — The earliest Musk Deer of the genus *Moschus* and their significance in clarifying of evolution and relationships of the family Moschidae. *Paleontological Journal* 43 (3): 87-99. https://doi.org/10.1134/S0031030109030125

WALLACE A. R. 1876. — *The Geographical Distribution of Animals*. Vols 1 and 2. Harper & Brothers, New York. https://doi.org/10.5962/bhl.title.42326

WANG S., SHI Q., HUI Z., LI Y., ZHANG J. & PENG T. 2015. — Diversity of Moschidae (Ruminantia, Artiodactyla, Mammalia) in the Middle Miocene of China. *Paleontological Research* 19: 143-155. https://doi.org/10.2517/2014PR032

WEBB S. D. & TAYLOR B. E. 1980. — The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bulletin of the American Museum of Natural History* 167: 117-158. http://hdl.handle.net/2246/1042

WIRTH V. 1995. — *Die Flechten Baden-Wurttembergs*. 2 ed., Stuttgartp.

XIANG Z.-F., LIANG W.-B., NIE S.-G. & LI M. 2012. — Diet and Feeding Behavior of *Rhinopithecus brelichi* at Yangaoping, Guizhou. *American Journal of Primatology* 74: 551-560. https://doi.org/10.1002/ajp.22008

ZAITSEV V. A., SERYODKIN I. V., MAKSIMOVA D. A. & SOUTYRINA S. V. 2015. — Study of the Musk Deer Population Structure in Sikhote-Alin Reserve. *Achievements in the Life Sciences* 9: 83-86. https://doi.org/10.1016/j.als.2015.11.001

ZEDDA L. 2002. — The Epiphytic Lichens on *Quercus* in Sardinia (Italy) and Their Value as Ecological Indicators. *Englera* 24: 3-457. https://doi.org/10.2307/3776783

ZHANG J., ZHOU Y., XU W., HU J. & LIAO W. 2004. — Discussion about musk-deer's classification. *Journal of Sichuan Teachers College (Natural Science)* 25: 251-255.

ZHAO H., DANG G., WANG C., WANG X., GUO D., LUO X., ZHAO J., HE Z. & LI B. 2015. — Diet and seasonal changes in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the southern Qinling mountains in China. *ACTA Theriologica Sinica* 35: 130-137.

ZHIXIAO L. & HELIN S. 2002. — Effect of Habitat Fragmentation and Isolation on the Population of Alpine Musk Deer. *Russian Journal of Ecology* 33: 121-124. https://doi.org/10.1023/A:1014456909480

Submitted on 10 September 2018;
accepted on 31 December 2018;
published on 9 May 2019.