# Feeding ecology of the Chalicotheriidae (Mammalia, Perissodactyla, Ancylopoda).
# Results from dental micro- and mesowear analyses

By

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With 6 Figures 7 Tables and 3 Appendices

Abstract: The Chalicotheriidae are extinct, large, claw-bearing Perissodactyls. There are two subfamilies, the Chalicotheriinae and the Schizotheriinae. These are discerned by the more derived cheek dentition and also by more primitive postcranial anatomy of the latter. The Chalicotheriidae are commonly reconstructed as leaf-eating herbivores. For the first time the analysis of dental mesowear and microwear have been employed to infer palaeodiets of members of both subfamilies. Two species of the Chalicotheriinae (*Chalicotherium* (*Anisodon*) *grande* and *Chalicotherium goldfussi*), and two species of the Schizotheriinae (*Metaschizotherium fraasi* and *Metaschizotherium* sp.) deriving from 20 Miocene vertebrate localities of Southern Germany were analysed. These localities represent the Upper Freshwater Molasse (MN 5 to MN 9), the karst plateau of the Franconian Alb (MN 6), and the Dinotheriensande complex (MN 9). Microwear signatures suggest a strong browse component, which is different from that in extant browsing ruminants. Based on the microwear data, graminoids can be excluded as an abrasive dietary component. Mesowear signatures indicate a highly abrasive component like bark, twigs and branches in the diet of the chalicotheres while microwear suggests unusual browsing components. We thus challenge the common assumption of chalicotheres solely living on browse and conclude an intermediate feeding dietary trait. A diet including a substantial amount of bark and twigs would be strongly supported by specialisations seen in the morphology of the Chalicotheriinae, e.g. pronounced insertion surfaces for the masticatory muscles on the mandible, shortened hind limbs, protractible forelimbs and large ungual phalanges. The Schizotheriinae investigated had a less abrasive diet, and would be characterised as intermediate feeders based on their mesowear signatures. A feeding behaviour connected to a diet composed of mixed forage may be reflected in the less extreme development or missing of the above mentioned morphological characters.

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# A. Introduction

Ever since the Chalicotheriidae had been mentioned for the first time (cf. Cuvier 1823) their peculiar anatomy has fascinated biologists and palaeontologists. The family is known to have existed on all continents with the exception of South America and Australia. They were present in Eurasia from the Palaeogene until the early Pleistocene (Coombs 1989). Two subfamilies, the Chalicotheriinae and the Schizotheriinae, are distinguishable by their morphological characters (Coombs 1989). The molars of the Chalicotheriidae in general are described as brachyodont and bunoselenodont (e.g. Zapfe 1979), but in the Schizotheriinae they are comparably higher crowned and more elongate than in the Chalicotheriinae (cf. Koenigswald 1932; Zapfe 1979; Coombs 1989). Both groups also strongly differ in their postcranial skeletal anatomy. Subequal proportions of fore- and hind limbs are retained in the Schizotheriinae whereas the Chalicotheriinae have remarkably short hindlimbs and a protractable humerus as derived characteristics. Therefore, the posture of the latter group is often described as rather "gorilla-like" (Zapfe 1979; Coombs 1989) (Fig. 1). Although differing between both subfamilies in their robustness, the large bifurcal, laterally compressed ungual phalanges, probably bearing huge claws, are considered to be a shared morphological adaptation for dragging or tearing down branches. In consideration of these characters, the Chalicotheriidae are mostly reconstructed as leaf-eaters (e.g. Koenigswald 1932; Zapfe 1976, 1979; Coombs 1982, 1989; Heissig 1999).

Approaches to the diets of extinct mammals involve ecomorphology (e.g. Janis & Fortelius 1988; Solounias & Moelleken 1993; Solounias et al. 1995) and complementary taxon free methods as stable isotopes (e. g. Zazzo et al. 2000; Zazzo et al. 2002; Sponheimer et al. 2003; Merceron et al. 2006), dental mesowear (e.g. Solounias et al. 1994; Fortelius & Solounias 2000; Kaiser & Fortelius 2003; Kaiser & Solounias 2003), and dental microwear analysis (e.g. Caprini 1998; MacFadden et al. 1999; Merceron & Ungar 2005; Merceron et al. 2006; Kaiser & Brinkmann 2006). The absence of modern relatives of the Chalicotheriidae has always made it difficult, however, to reconstruct their ecology.

Two major working hypotheses are therefore tested by this study:

1. The Chalicotheriidae have a dietary adaptation similar to extant browsing herbivores (e.g. Koenigswald 1932; Zapfe 1976, 1979; Coombs 1982, 1989; Heissig 1999).

2. Postcranial anatomical differences between the Chalicotheriinae and the Schizotheriinae reflect differences in feeding traits.

In order to cover both, long time dietary signals as well as short time signals, two tooth based taxon free approaches to palaeodiet have been combined here: 1. dental mesowear analysis and 2. dental microwear analysis.
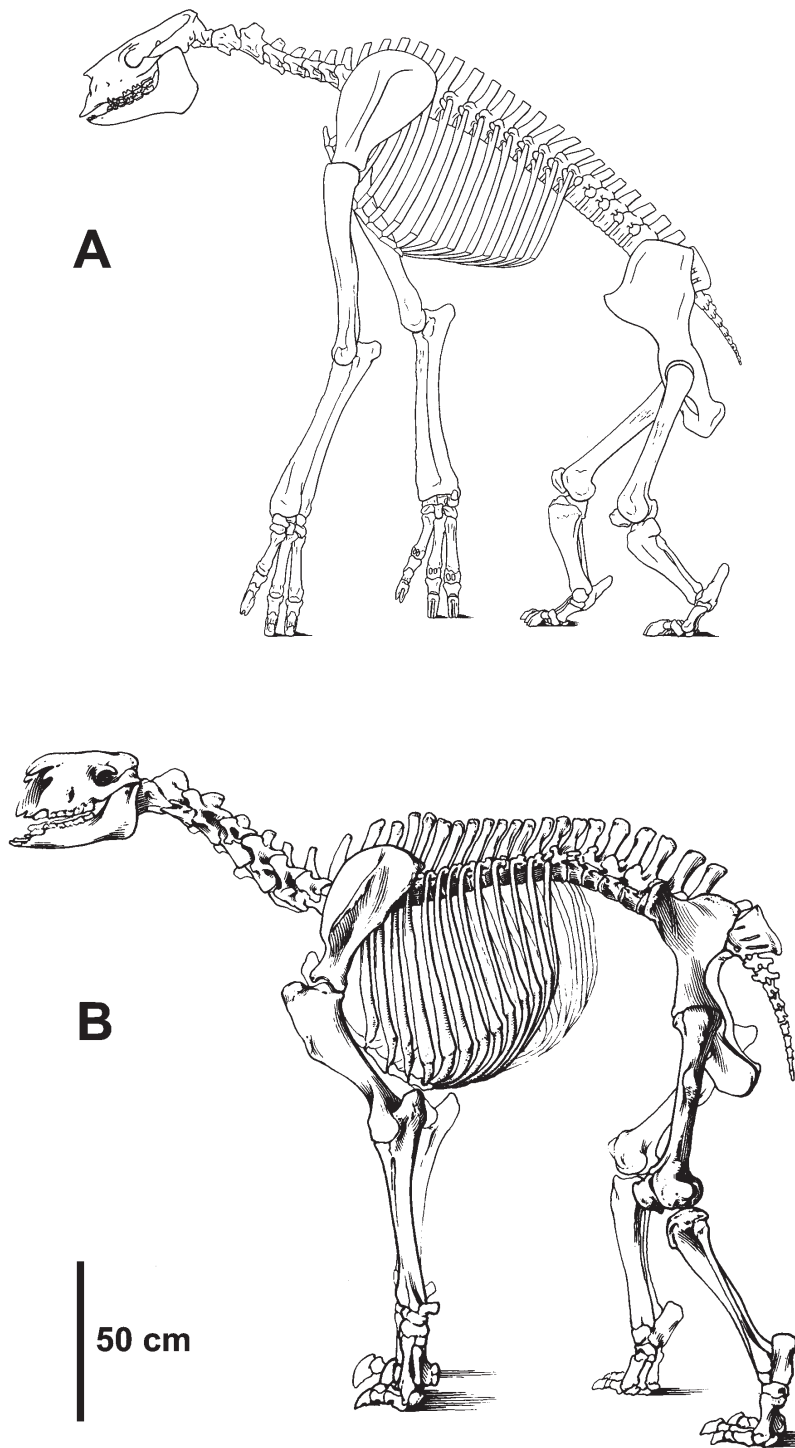
Fig. 1: Skeletal reconstruction of representatives of the Chalicotheriinae and the Schizotheriinae. *A*: Chalicotheriinae: *Chalicotherium* (*Anisodon*) *grande* after Zapfe (1979). *B*: Schizotheriinae: *Moropus elatus* after Osborn (1919).

# I. Dental mesowear analysis

The mesowear method of Fortelius & Solounias (2000) has proven to be a powerful tool for reconstructing dietary traits of herbivorous ungulates (Kaiser et al. 2000). It is based on facet development of cheek tooth occlusal surfaces. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food-to-tooth contact (abrasion). Attrition creates facets while abrasion obliterates them.
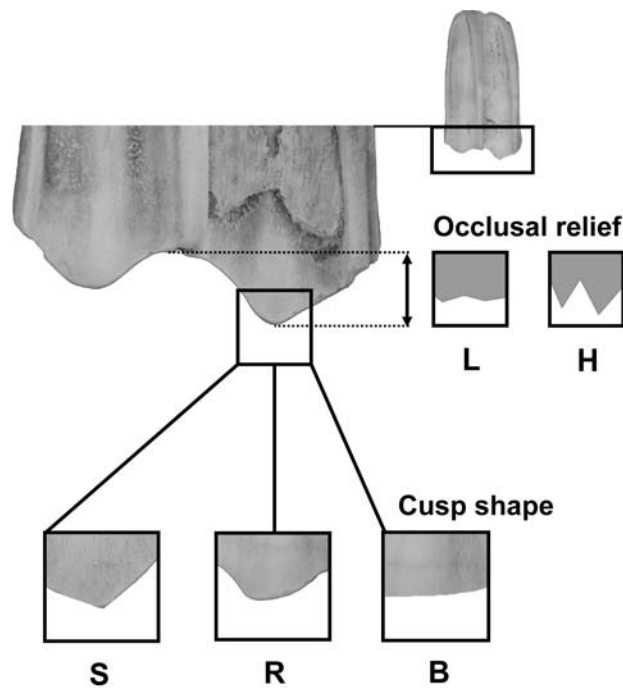


Fig. 2: The mesowear scoring convention for hypsodont ungulate cheek teeth as defined by Fortelius & Solounias (2000) for upper second molars. The occlusal relief may be scored "high" (*H*) or "low" (*L*), the cusp shape is classified as "sharp" (*S*), "round" (*R*), and "blunt" (*B*) (modified after Kaiser & Fortelius 2003).

The entire surface of the teeth is affected by tooth wear but mesowear analysis has focused on the buccal cutting edges of the enamel surfaces where the buccal wall (ectoloph) meets the occlusal surface. The mesowear method treats ungulate tooth mesowear as two variables: occlusal relief and cusp shape (Fig. 2). Occlusal relief (OR) is classified as high (H) or low (L), depending on how high the cusps rise above the valley between them. The second mesowear variable, cusp shapes, includes 3 scored attributes: sharp (S), round (R) and blunt (B) according to the degree of facet development. Attrition results in high occlusial reliefs, abrasion in low reliefs. Abrasion also creates rounded and blunt cusp apices, attrition creates sharp cusps. The method after Fortelius & Solounias (2000) investigates mesowear using the upper second molar ($M^2$) as a model. Kaiser & Solounias (2003) extended the method to four tooth positions ($P^4$–$M^3$) in order to make it available for fossil equid assemblages. The tooth model was further extended to lower molars in equids (Kaiser & Fortelius 2003) and to both upper M2 and M3 in ruminants (Franz-Odendaal & Kaiser 2003).

Mesowear analysis has so far been successfully employed to fossil equids and ruminants, respectively (e.g. Fortelius & Solounias 2000; Franz-Odendaal et al. 2003; Kaiser 2003; Kaiser & Fortelius 2003; Kaiser & Solounias 2003; Franz-Odendaal & Solounias 2004; Kaiser & Croitor 2004).

Extant grazing ungulates usually have low occlusal reliefs and round or blunt cusps. Browsers on the other extreme tend to have high occlusal reliefs and sharp or round cusps (Fortelius & Solounias 2000).

## II. Dental microwear analysis

The dental microwear method is based on the quantification of microwear scars on the enamel surface of teeth. These scars are dichotomized into either round (pits) or elongate (scratches). Sizes and densities of these microwear scars allow to infer the physical properties of the last meals (Walker et al. 1978; Teaford & Oyen 1989). Grazers usually have higher ratios of scratches over pits (Solounias & Semprebon 2002; Merceron et al. 2004a; Merceron et al. 2006) due to the consumption of monocotyledons which may contain high concentrations of silica phytoliths (cf. Kaufman et al. 1985; Carnelli et al. 2001). This increased abrasiveness is also seen as an adaptive response to increased grazing by ungulates (MacNaughton et al. 1985). Browsing ungulates feed on a variety of dicotyledons, which mostly contain far less phytoliths. Browsers thus have higher pit percentage values (Solounias & Semprebon 2002; Merceron et al. 2004a; Merceron et al. 2006). Beyond the grazer/browser dichotomy, the dental microwear design may reveal more specific feeding preferences. For instance, a qualitative trend is recognized among browsers. The ones whose diet may contain a larger amount of fruits or seeds (here termed as fruit browsers) have significantly more scratches than the browsers that mainly or totally feed on leaves (here termed as leaf browsers) (Solounias & Semprebon 2002; Merceron et al. 2004a; Merceron et al. 2006). Some species have a dental microwear pattern that overlaps with the range of values scored for both grazers and browsers. Some of them have a marked bimodal distribution of the main microwear variables (Solounias & Moelleken 1992; Solounias & Semprebon 2002; Merceron et al. 2004a; Merceron et al. 2006). This peculiar pattern is seen on species whose feeding preferences strongly and swiftly vary from browsing to grazing on a seasonal basis. These ungulates are here termed as "seasonal mixed-feeders". Some other species show high densities of both scratches and pits without showing bimodal patterns and in that are different from seasonal mixed feeders. This dental microwear signature is recognized in many ungulates engaged in both grazing and browsing on a daily basis. Solounias & Semprebon (2002) termed this group of extant ungulates as "meal by meal" mixed feeders. Here we prefer the term "generalists" instead. So we distinguish five major feeding types among extant ungulates which may be recognized by dental microwear analysis: 1. grazers, 2. leaf browsers, 3. fruit browsers, 4. generalists, and 5. seasonal mixed-feeders. All these reflect associated ecological data.

# B. Material

The fossil specimens analyzed (Appendix 1) are housed in the following museum collections: 1. Bayerische Staatssammlung für Paläontologie und historische Geologie Munich (BSP), 2. collection of Dr. M. Rummel, Augsburg (MR), 3. Naturmuseum Augsburg (NMA), and 4. Hessisches Landesmuseum Darmstadt (HLMD). The material includes remains of four species of the Chalicotheriidae deriving from 20 different Miocene localities in Southern Germany: *Chalicotherium goldfussi* Kaup, 1833 from several localities of the Dinotheriensande complex, MN 9 (n = 22), *Chalicotherium (Anisodon) grande* de Blainville, 1849 from several localities of the Upper Freshwater Molasse, MN 5 to MN 6 and MN 8 to MN 9 (n = 16), *Metaschizotherium* sp. Koenigswald, 1932 from the Lower Middle Miocene Upper Freshwater Molasse deposits of Sandelzhausen, MN 5 (Heissig 1997) (n = 11), and *Metaschizotherium fraasi* Koenigswald, 1932 form the karst fissure filling Petersbuch 71, MN 6 (n = 4).

The systematics and taxonomy of the Chalicotheriinae are currently under revision (J. Anquetin, pers. comm.; cf. Bonis et al. 1995). In order to not foresight ongoing research, we here tentatively use the name *Chalicotherium (Anisodon) grande* for the chalicotheriine remains from the Upper Freshwater Molasse of Southern Germany (MN 5 to MN 6 and MN 8 to MN 9). The material from the MN 5 of Sandelzhausen was initially described as *Chalicotherium* (Fahlbusch et al. 1972). Its schizotheriine nature was later recognized by Coombs (1974). It can clearly be distinguished from *M. fraasi* on a morphological basis, but a redescription of the Sandelzhausen material by M. Coombs is still to follow (M. Coombs, pers. comm.). We therefore use the term '*Metaschizotherium* sp.' for the Sandelzhausen material.

# C. Methods

## I. Mesowear analysis

According to the mesowear convention by (Fortelius & Solounias 2000) the sharper buccal cusp of a cheek tooth (either the paracone or the metacone) is scored. In order to increase the number of observations we slightly modify the scheme here, in that we include both, the anterior and the posterior buccal cusps into our analysis. The teeth were examined with naked eye and using a low magnification (10x) hand lens. Cusp shape and occlusal relief variables were scored according to the convention of Fortelius & Solounias (2000). Some specimens show obvious taphonomic alterations, such as severe abrasion due to transport in a river bed. Cusp shape variables of such specimens could not be recorded. However, occlusal relief scorings were collected. Owing to this bias, sample sizes vary between occlusal relief and cusp shape scorings (Tab. 1).

Tab. 1: Mesowear variable frequencies expressed as absolute counts and percentages of upper $P^4$, $M^1$, $M^2$ and $M^3$ of *Chalicotherium goldfussi*, *Chalicotherium (Anisodon) grande*, *Metaschizotherium* sp. and *Metaschizotherium fraasi* from the Miocene of Southern Germany.

| | absolute counts | | | | percentages | | | | | |
| | OR | | CS | | | OR | | | CS | |
| species | L | H | S | R | B | %L | %H | %S | %R | %B |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chalicotherium goldfussi* | 2 | 22 | 1 | 14 | 1 | 8.3 | 91.67 | 6.25 | 87.50 | 6.25 |
| *Chalicotherium (Anisodon) grande* | 2 | 14 | 2 | 12 | 1 | 12.5 | 87.5 | 13.3 | 80.0 | 6.75 |
| *Metaschizotherium* sp. | 0 | 11 | 4 | 5 | 0 | 0 | 100 | 44.4 | 55.6 | 0 |
| *Metaschizotherium fraasi* | 0 | 4 | 2 | 2 | 0 | 0 | 100 | 50 | 50 | 0 |

Percentages of mesowear variable frequencies (%high, %sharp and %blunt) were calculated and cluster analyses performed to allow comparison with extant species as published by Fortelius & Solounias (2000) (Appendix 2). This database of extant species is different from the one employed in microwear analysis. Hierarchial cluster statistics with complete linkage (furthest neighbours) were calculated using Systat 11.0 (SYSTAT Software Inc., Richmond, CA) software and following the standard hierarchical amalgamation method of Hartigan (1975). The algorithm of Gruvaeus & Wainer (1972) was then used to order the cluster tree using the three mesowear variables (% high, % sharp and % blunt). As a comparative dataset for dietary classification, we follow Fortelius & Solounias (2000) and Kaiser & Solounias (2003) and use a set of 2007 wild-shot adult ungulate specimens representing 61 extant species. We follow Fortelius & Solounias (2000) conservative (CONS) classification of species in dietary categories as grazers, browsers or mixed feeders. In this classification species are distinguished by the ad hoc classifying variable class with the values "no particular class" (no), "minute abraded brachyodont" (mabra) and "typical of its dietary class" (typical). Following this classification we computed two cluster trees: Fig. 3A compares the Chalicotheriidae with the 27 "typical" extant species; Fig. 3B includes 61 "typical", "mabra" and "no" species (Fig. 3B).

Instead of the term "mixed feeder" the term "intermediate feeder" is preferred here in order to avoid confusions with the terms employed in the following chapter. The intermediate feeder category in the mesowear scheme comprises both, seasonal mixed feeder and generalists categories used in the microwear scheme.

## II. Microwear analysis

Many fossils were too fragile for moulding and thus could not be included into dental microwear analysis. Other specimens had to be excluded, as they were obviously physically altered during transportation or compaction of sediments (cf. King et al. 1999). Due to the reduced number of specimens, only the two Chalicotheriinae *Chalicotherium goldfussi* (n = 20) and *Chalicotherium (Anisodon) grande* (n = 11) were considered (Appendix 1).

As extant comparative data we employ a set of 525 wild-shot adult individuals representing 32 living species (Merceron et al. 2004a; Merceron et al. 2005c; Merceron et al. 2005b). These species represent the five major diet categories as mentioned above (Appendix 3). All microwear investigation was undertaken using high resolution resin casts rather than original teeth. Several research protocols for microwear analysis have been developed involving different casting protocols (Puech et al. 1983; Gordon 1984; Teaford & Oyen, 1989; Merceron et al. 2004a) and routines of data acquisition and analysis (Walker et al. 1978; Ungar 1996; Solounias & Semprebon 2002; Ungar et al. 2003; Merceron et al. 2005a; Merceron & Ungar 2005; Kaiser & Brinkmann 2006; Scott et al. 2006). Here the protocol of Merceron et al. (2004a, 2005a) is employed, which combines the convenience of light stereomicroscopy (Walker 1976; Solounias & Semprebon 2002) and the reliability of high-resolution image analyses (Ungar 1996). This protocol is currently widely being used for investigation of both, feeding behaviour and mastication processes of various mammals (Boisserie et al. 2005; Merceron et al. 2006; Charles et al. in press).

The anterior lingual blade of the paracone and the posterior buccal blade of the protoconid on second molars were considered. These facets occlude during the shearing masticatory phase I (Kay & Hiiemae 1974; Janis 1990). Because the dental microwear signature is not significantly different on occluding dental facets (Teaford & Walker 1984; Semprebon et al. 2004), both upper and lower second molars were considered.

Molar phase I shearing facets were digitized using a camera (Leica DC 300) and acquisition software (Leica IM 500), connected to a light stereomicroscope (Leica MZ 16) at low magnification (x30). Prior to exposure the contrast was adjusted using a pivoting mirror, which slightly tilts the beam of incident light. This mirror is located under the platform where the transparent facet replica is mounted. The magnification was subsequently increased up to 120 times for treatment on the computer monitor (Merceron et al. 2004a; Merceron et al. 2004b; Merceron et al. 2005a). Then, dental microwear was quantified in a 0.09 mm$^2$ (300 x 300 µm) square area using Optimas 6.2 image analyses software (Media Cybernetics®). Microwear scars were then defined as pits or scratches as follows: pits have a width to length ratio higher than $^1/_4$ and scratches have a lower one

(GRINE 1986). Using Optimas 6.2, pits were marked with points and scratches with lines that are cords linking scratch extremities. This means that curve parameters were not considered in the present analysis. The length of a cord is scored as length of a scratch (Ls). After scoring the number of pits (Np) and the number of scratches (Ns), the total number of microwear scars (Tot = Ns + Np) and the percentage of pits (Pp = Np/Tot) were computed (Tab. 2). Statistical analyses were undertaken in order to test if the observed inter-group differences of microwear patterns were significant. Because normality and homeoscedasticity are not guaranteed, all variables were rank-transformed. Univariate analyses of variances (ANOVAs, Tab. 3, 5) were applied to test significance of observed differences between samples (CONOVER & IMAN 1981; SCHERRER 1984; SOKAL & ROHLF 1998). The Scheffé multiple comparisons test was used to determine sources of significant variation (Tab. 4). The null hypotheses stipulate that the samples have similar microwear patterns. Non-parametric Kolmogorov-Smirnov test was further applied to two sets of *Chalicotherium* (*Anisodon*) *grande* as defined by their stratigraphic assignation, MN 5 to MN 6 versus MN 8 to MN 9 (Tab. 6, 7).

Tab. 2: Summary statistics (mean and sem = standard error of the mean) of dental microwear variables of extant taxa according to their dietary category and the extinct species *Chalicotherium* (*Anisodon*) *grande* and *Chalicotherium goldfussi* from the Miocene of Southern Germany.

| | n | Pp | | Ns | | Ls | | Np | | Tot | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mean | sem | mean | sem | mean | sem | mean | sem | mean | sem |
| Seasonal mixed feeders [E] | 41 | 51.3% | 2.0% | 21.5 | 1.1 | 138.2 | 8.3 | 23.9 | 1.8 | 45.4 | 2.3 |
| Grazers [E] | 161 | 35.7% | 0.9% | 25.0 | 0.4 | 171.1 | 3.3 | 15.2 | 0.7 | 40.2 | 0.9 |
| Leaf browsers [E] | 44 | 65.3% | 1.3% | 17.3 | 0.6 | 155.2 | 4.7 | 35.9 | 1.9 | 53.2 | 2.0 |
| Fruit/leaf browsers [E] | 231 | 59.2% | 0.9% | 22.1 | 0.5 | 130.7 | 2.8 | 33.9 | 1.1 | 56.0 | 1.2 |
| Generalists [E] | 104 | 57.8% | 1.7% | 26.4 | 0.9 | 160.6 | 4.4 | 40.7 | 2.0 | 67.1 | 1.9 |
| *Chalicotherium* (*Anisodon*) *grande* † | 11 | 83.8% | 4.6% | 13.7 | 2.9 | 93.9 | 15.1 | 87.9 | 12.7 | 101.5 | 11.6 |
| *Chalicotherium goldfussi* † | 20 | 75.2% | 2.9% | 16.5 | 2.0 | 158.6 | 17.4 | 52.8 | 5.0 | 69.3 | 5.9 |

Variables are as follows: $N$ = number of specimens, $Pp$ = percentage of pits, $Ns$ = number of scratches, $Ls$ = length of scratches (μm), $Np$ = number of pits, and $Tot$ = total number of microwear scars. [E] diet categories based on extant species from the "Ungulates" database (MERCERON et al. 2004a, 2005b, 2005c, 2006); † fossil taxa.

Tab. 3: Analyses of variance (ANOVAs) with ranked data. Categorial variables: dietary categories and fossil species.

| | | df | SS | MS | F | p |
|---|---|---|---|---|---|---|
| **Pp** | Effect | 6 | 7533091 | 1255515 | 84.445 | 0.00 |
| | Error | 605 | 8474655 | 14868 | | |
| **Tot** | Effect | 6 | 5145904 | 857651 | 45.029 | 0.00 |
| | Error | 605 | 10856488 | 19046 | | |
| **Ns** | Effect | 6 | 3197877 | 532980 | 23.7657 | 0.00 |
| | Error | 605 | 12783080 | 22426 | | |
| **Ls** | Effect | 6 | 2686774 | 447796 | 19.1603 | 0.00 |
| | Error | 605 | 13321514 | 23371 | | |
| **Np** | Effect | 6 | 6885833 | 1147639 | 71.765 | 0.00 |
| | Error | 605 | 9115199 | 15992 | | |

Variables are as follows: $Pp$ = percentage of pits, $Tot$ = total number of microwear scars, $Ns$ = number of scratches, $Ls$ = length of scratches (μm), $Np$ = number of pits. $df$ = degree of freedom, $SS$ = Sum of squares,

$MS$ = mean square (SS/df), $F$ ratio = $MS$ for the considered factor/$MS$ of the Residual ( = Error), $p$ = probablity it to reject the null hypothesis (that stipulate equal samples) at 95% while p is lower than 0.05.

Tab. 4: Scheffé multicomparison test of the extinct species *Chalicotherium* (*Anisodon*) *grande* and *Chalicotherium goldfussi* with extant taxa according to their dietary categories. **bold**: significantly lower than data of extant species, normal font: significantly higher than data of extant species.

|  | Seasonal mixed feeders | Grazers | Traditional browsers | Fruit browsers | Generalists |
|---|---|---|---|---|---|
| *Chalicotherium* (*Anisodon*) *grande* | Pp Tot Np | Pp Tot **Ns Ls** Np | Pp Tot **Ls** | Pp Tot Np | Pp **Ns Ls** Np |
| *Chalicotherium goldfussi* | Pp Tot Np | Pp Tot **Ns** Np |  | Pp Np | Pp **Ns** |

Variables are as follows: $Ns$ = number of scratches, $Ls$ = length of scratches (μm), $Np$ = number of pits, $Pp$ = percentage of pits, and $Tot$ = total number of microwear scars.

Tab. 5: ANOVAs of ranked data to test the significance of the observed microwear differences from $M^1$ to $M^3$ of *Chalicotherium goldfussi*.

|  |  | df | SS | MS | F | p |
|---|---|---|---|---|---|---|
| **Pp** | Effect | 2 | 12619 | 6310 | 0.432 | >0.05 |
|  | Error | 15 | 218825 | 14588 |  |  |
| **Tot** | Effect | 2 | 40139 | 20070 | 0.6055 | >0.05 |
|  | Error | 15 | 497181 | 33145 |  |  |
| **Ns** | Effect | 2 | 104748.5 | 52374.3 | 1.648 | >0.05 |
|  | Error | 15 | 476704.9 | 31780.3 |  |  |
| **Ls** | Effect | 2 | 64676.1 | 32338.1 | 0.645 | >0.05 |
|  | Error | 15 | 751825.9 | 50121.7 |  |  |
| **Np** | Effect | 2 | 22591 | 11295 | 0.561 | >0.05 |
|  | Error | 15 | 302004 | 20134 |  |  |

Variables are as follows: $Pp$ = percentage of pits, and $Tot$ = total number of microwear scars, $Ns$ = number of scratches, $Ls$ = length of scratches (μm), $Np$ = number of pits, $df$ = degree of freedom, $SS$ = Sum of squares, $MS$ = mean square ($SS/df$), $F$ ratio = $MS$ for the considered factor/$MS$ of the Residual ( = Error), $p$ = probablity it to reject the null hypothesis (that stipulate equal samples) at 95% while $p$ is lower than 0.05.

Tab. 6: Summary statistics (mean and sem = standard error of the mean) on dental microwear variables of *Chalicotherium* (*Anisodon*) *grande* according to the stratiphigraphic level.

|  | N | Ns mean | Ns sem | Ls mean | Ls sem | Np mean | Np sem | Pp mean | Pp sem | Tot mean | Tot sem |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total | 11 | 13.7 | 2.9 | 93.9 | 15.1 | 87.9 | 12.7 | 83.8% | 4.6% | 101.5 | 11.6 |
| MN 8 – MN 9 | 4 | 21.1 | 5.2 | 101.3 | 40.2 | 65.1 | 18.1 | 71.5% | 9.9% | 86.3 | 13.4 |
| MN 5 – MN 6 | 7 | 9.4 | 2.3 | 89.7 | 11.2 | 100.9 | 15.9 | 90.9% | 2.0% | 110.3 | 16.2 |

Variables are as follows: $N$ = number of specimens, $Ns$ = number of scratches, $Ls$ = length of scratches (μm), $Np$ = number of pits, $Pp$ = percentage of pits, $Tot$ = total number of microwear scars.

Tab. 7: Non-parametric Kolmogorov-Smirnov test of the specimens of *Chalicotherium* (*Anisodon*) *grande*; MN 5–6 versus MN 8–9.

| | Maximum Differences | | |
|---|---|---|---|
| | Negative | Positive | p |
| Ns | -0.71 | 0.00 | p > 0.10 |
| Ls | -0.25 | 0.50 | p > 0.10 |
| Np | 0.00 | 0.75 | p > 0.10 |
| Pp | 0.00 | 0.75 | p > 0.10 |
| Tot | -0.18 | 0.43 | p > 0.10 |

Variables are as follows: *Ns* = number of scratches, *Ls* = length of scratches (μm), *Np* = number of pits, *Pp* = percentage of pits, *Tot* = total number of microwear scars, *p* = probablity to reject the null hypothesis (that stipulate equal samples) at 95% while *p* is lower than 0.05.

# C. Results

## I. Mesowear analysis

Bar charts (Fig. 4) indicate similar occlusal relief frequencies in *Chalicotherium goldfussi* and *Chalicotherium* (*Anisodon*) *grande* (Tab. 1, Fig. 4A, B), but more sharp cusps are recorded in *C.* (*A.*) *grande*. In cluster plots (Fig. 3A, B) *C. goldfussi* and *C.* (*A.*) *grande* are closely linked with grazing extant species. *C. goldfussi* plots closest to the African bovid *Redunca redunca* (PALLAS, 1767) and is rooted in the same sub-cluster as *C.* (*A.*) *grande* (Fig. 3A).

The schizotheriines (*Metaschizotherium*) classify within the spectrum of extant intermediate feeders. *Metaschizotherium* sp. is linked closest to *Cervus elaphus canadensis* ERXLEBEN, 1777 (Fig. 3A). Both species have 100% high occlusal relief and no blunt cusps (Fig. 4C, D). *Metaschizotherium fraasi* has a mesowear pattern similar to those of *Taurotragus oryx* (PALLAS, 1766) (Fig. 4G) and *Tragelaphus scriptus* (PALLAS, 1766) (Fig. 4H). All these are intermediate feeders and share a common sub-cluster neighbouring the cluster containing *Metaschizotherium* sp. (Fig. 3A).

Fig. 3A only contains extant species classified as "typical" dietary categories following the conservative (CONS) classification of FORTELIUS & SOLOUNIAS (2000). The peculiar post cranial and cranial anatomy of the Chalicotheriinae however suggests different feeding habits compared to the species defined as "typical" by FORTELIUS & SOLOUNIAS (2000). In fact, these extant reference species may not fully cover the potential dietary traits of the group. We therefore include all extant reference species which FORTELIUS & SOLOUNIAS (2000) classify as "no particular class" and "mabra" feeding groups, into our second cluster analysis (Fig. 3B). In Southern Germany *Chalicotherium* (*A.*) *grande* spans a temporal range from MN 5–6 to MN 8–9. We therefore investigate individual sub-groups of *C.* (*A.*) *grande* as related to stratigraphic levels.

The integration of the "no" and "mabra" categories of extant species into the dendrogram does not result in a strict separation of feeding groups (Fig. 3B), but intermediate feeders may be placed between or within grazers and browser (Fig. 3B).

In Fig. 3B *Chalicotherium goldfussi* (MN 9) is classified close to the "typical" grazer *Redunca redunca* while *Chalicotherium* (*Anisodon*) *grande* has two distinct classification patterns depending on the MN zones they represent. Specimens from the MN 5–6 are closely linked to *Gazella granti* Brooke, 1872, *G. thomsoni* Günther, 1884 and *Ovibos moschatus* Zimmermann, 1870. These three extant bovids represent the dietary category of the "typical intermediate feeders" after Fortelius & Solounias (2000). The American bighorn sheep (*Ovis canadensis* Shaw, 1804) is the only intermediate feeder in this cluster classified as "no particular class" by Fortelius & Solounias (2000). However, the subgroup of *C.* (*A.*) *grande* from MN 5–6 is also linked to the western tree hyrax (*Dendrohyrax dorsalis* Fraser, 1852), a "mabra" species. The MN 8–9 sample of *C.* (*A.*) *grande* shows a clustering pattern similar to that in Fig. 3A. The closely linked *Redunca redunca* is a "typical" grazer, and *Cervus unicolor* Kerr, 1792 is classified as "no particular class" intermediate feeder by Fortelius & Solounias (2000). At a higher linkage level, three extant "mabra" species are closely linked to *Chalicotherium goldfussi* (MN9) and *C.* (*Anisodon*) *grande* from MN 8–9.

The linkage patterns of *Metaschizotherium fraasi* and *Metaschizotherium* sp. in Fig. 3B equal those in Fig. 3A. In addition, *Metaschizotherium* sp. is connected to the "no particular class" browser African bongo (*Tragelaphus euryceros* (Ogilby, 1837)). *M. fraasi* from MN 6 is also linked to the second hyrax species in this comparison, the southern tree hyrax (*Dendrohyrax arboreus* (A. Smith, 1827)). Two "mabra" species, *Hyaemoschus aquaticus* (Ogilby, 1841) and *Cephalophus natalensis* (A. Smith, 1834) are closely linked to the dominated grazer spectrum. Even more similarities with "mabra" species are evident in *M. fraasi* which is immediately linked to *Dendrohyrax arboreus* and the MN 5–6 sub-group of *C.* (*A.*) *grande* which is closely linked to *Dendrohyrax dorsalis*.

## II. Microwear analysis

*Description of dental microwear pattern of fossil species.* – Both species of *Chalicotherium* show a number of scratches (Ns) lower than that of living species (Fig. 5B; Tab. 2). *C. goldfussi* has scratches as long as living browsers whereas those of *C.* (*A.*) *grande* have shorter ones than all dietary categories based on extant species (Tab. 2). In both fossil species higher pit densities than living species have been observed; however *C.* (*A.*) *grande* has more pits than *C. goldfussi* (Fig. 5A, 5C). This implies that both Tot (Total number of microwear scars) and Pp (Percentage of pits) variables are higher for the fossil species than for any of dietary categories based on extant species (Tab. 2). *C.* (*A.*) *grande*, however, has higher values of Np (number of pits), Tot (total number of microwear scars) and Pp (percentage of pits) than *C. goldfussi* (Fig. 5A, 5C; Tab. 2).
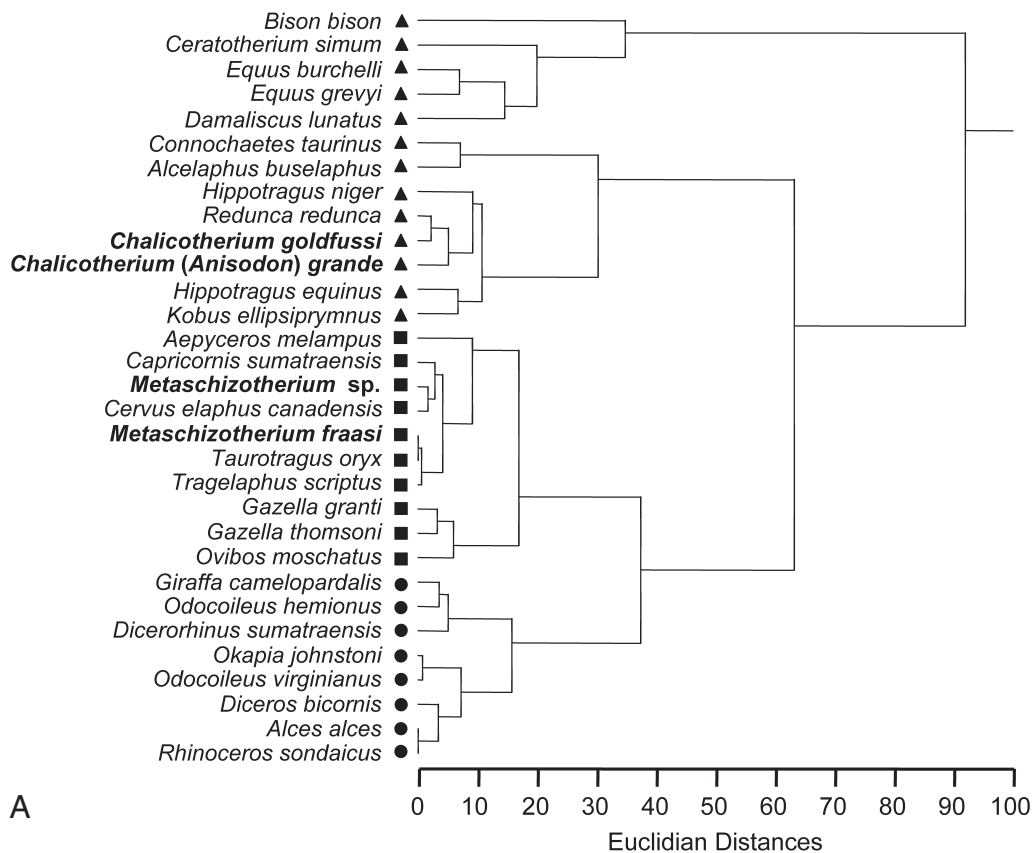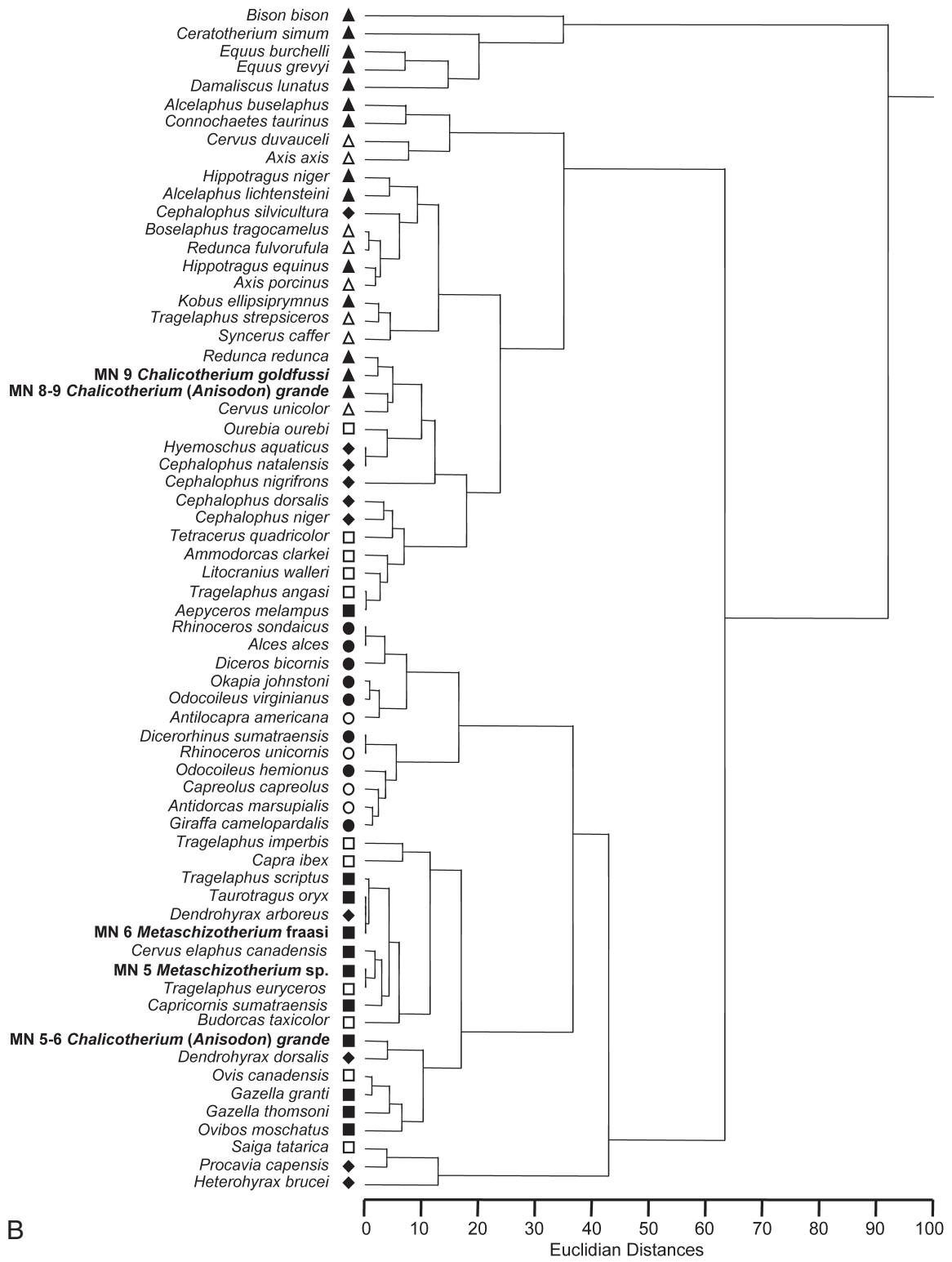
Fig. 3A, B: Hierarchical cluster diagrams plotting mesowear datasets of *Chalicotherium goldfussi*, *Chalicotherium* (*Anisodon*) *grande*, *Metaschizotherium* sp. and *Metaschizotherium fraasi* from the Miocene of Southern Germany together with 27 "typical" extant reference species after Fortelius & Solounias (2000) (**A**). – In addition (**B**) comprises "typical" (closed symbols), "no particular class" (open symbols) and "mabra" extant species. Symbols indicate dietary adaptations according to the consensus category by Fortelius & Solounias (2000): circle = browsers, rectangle = intermediate feeders, triangle = grazers, diamond = minute abraded brachydont ("mabra").

*Fossils species versus living taxa.* – ANOVA statistics indicate significant differences in all variables between samples (Tab. 3). The Scheffé multiple comparisons tests point out that *Chalicotherium* (*A.*) *grande* differs significantly from all diet categories in having higher Pp, Np and Tot values and have more similarities with leaf browsers (Fig. 6; Tab. 4; Fig. 5A, 5C). *C.* (*A.*) *grande* also differs from grazers and generalists in having fewer and shorter scratches (Tab. 4; Fig. 5B). The significant differences to leaf browsers concerning Pp and Tot are due to the very high pitting incidences on the shearing molar facets (Tab. 4; Fig. 5A, 5C). The Scheffé multiple comparison tests also indicate that *C. goldfussi* differs from all extant dietary categories, except for extant leaf browsers. In fact there are no significant differences between these Chalicotheriinae and the leaf browsers (Tab. 4; Fig. 5).
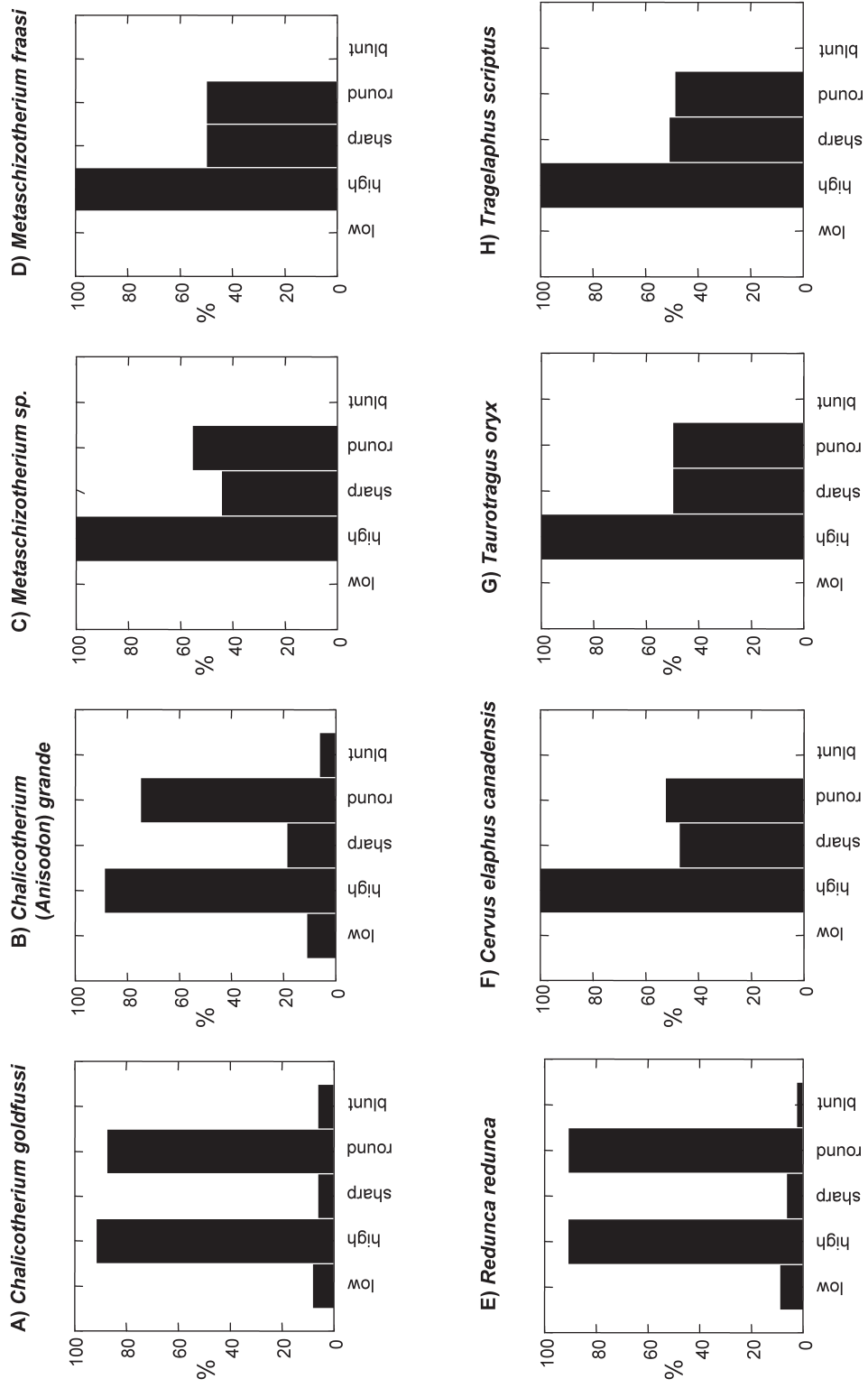
16

Bison bison ▲
Ceratotherium simum ▲
Equus burchelli ▲
Equus grevyi ▲
Damaliscus lunatus ▲
Alcelaphus buselaphus ▲
Connochaetes taurinus ▲
Cervus duvauceli △
Axis axis △
Hippotragus niger ▲
Alcelaphus lichtensteini ▲
Cephalophus silvicultura ◆
Boselaphus tragocamelus △
Redunca fulvorufula △
Hippotragus equinus ▲
Axis porcinus △
Kobus ellipsiprymnus ▲
Tragelaphus strepsiceros △
Syncerus caffer △
Redunca redunca ▲
**MN 9 *Chalicotherium goldfussi*** ▲
**MN 8-9 *Chalicotherium (Anisodon) grande*** ▲
Cervus unicolor △
Ourebia ourebi □
Hyemoschus aquaticus ◆
Cephalophus natalensis ◆
Cephalophus nigrifrons ◆
Cephalophus dorsalis ◆
Cephalophus niger ◆
Tetracerus quadricolor □
Ammodorcas clarkei □
Litocranius walleri □
Tragelaphus angasi □
Aepyceros melampus ■
Rhinoceros sondaicus ●
Alces alces ●
Diceros bicornis ●
Okapia johnstoni ●
Odocoileus virginianus ●
Antilocapra americana ○
Dicerorhinus sumatraensis ●
Rhinoceros unicornis ○
Odocoileus hemionus ●
Capreolus capreolus ○
Antidorcas marsupialis ○
Giraffa camelopardalis ●
Tragelaphus imperbis □
Capra ibex □
Tragelaphus scriptus ■
Taurotragus oryx ■
Dendrohyrax arboreus ◆
**MN 6 *Metaschizotherium* fraasi** ■
Cervus elaphus canadensis ■
**MN 5 *Metaschizotherium* sp.** ■
Tragelaphus euryceros □
Capricornis sumatraensis ■
Budorcas taxicolor □
**MN 5-6 *Chalicotherium (Anisodon) grande*** ■
Dendrohyrax dorsalis ◆
Ovis canadensis □
Gazella granti ■
Gazella thomsoni ■
Ovibos moschatus ■
Saiga tatarica □
Procavia capensis ◆
Heterohyrax brucei ◆

B

0   10   20   30   40   50   60   70   80   90   100
Euclidian Distances

17

Fig. 4: Percentages of mesowear variables of the fossil chalicotheriid and extant reference species.

*Fossils versus fossils.* – Within the Chalicotheriinae, no significant differences between molar positions (M1, M2 and M3) have been found (Tab. 5). According to the Kolmogorov-Smirnov test, there are no significant differences between the stratigraphically grouped (MN 5–6 and MN 8–9) samples of *C.* (*A.*) *grande* (Tabs. 6 and 7).

# D. Discussion

## I. Feeding preferences of the Chalicotheriidae – the dental evidence (hypothesis 1)

The long-term dietary signal provided by dental mesowear signatures indicates that both Chalicotheriinae (*Chalicotherium goldfussi* and *Chalicotherium* (*Anisodon*) *grande*) had a diet composed of abrasive plant material, which was similar in abrasiveness to that consumed by modern grazing antelopes. On the other hand, we find a pit dominated microwear pattern with low numbers of scratches in the Chalicotheriinae investigated here. A similar microwear signature was not found in any of the extant feeding groups (Tab. 2; Fig. 5). The observed low numbers of scratches places *C.* (*A.*) *grande* and *C. goldfussi* closest to the group of extant leaf browsers as defined by Merceron et al. (2004b, 2005b, 2005c, 2006). The low numbers of scratches also suggest that none of the two chalicotheriines had ingested a substantial amount of graminoids. This suggests, that the abrasive component, as indicated by the mesowear signal, is not related to a grass component in the diet. Owing to the very low scratch density, we can also exclude distinct frugivory as a feeding strategy of the Chalicotheriinae and conclude that fruit in general, including hard seeded fruit was not a major element of their diet (Fig. 6A – B). The abrasion dominated mesowear signature together with a microwear signature indicating leaf browsing is considered strong evidence, that none of the extant feeding categories matches the dietary trait of the Chalicotheriinae. Fortelius & Solounias (2000) grouped a set of extant ungulate species as "minute abraded brachydonts" (mabra) in their mesowear convention. These species share a high frequency of high occlusal reliefs with browsers, but also a high frequency of rounded cusps with intermediate feeders, and even with some grazers (Fortelius & Solounias 2000: 4). This indicates a strong abrasive component in the diet of these "mabra" species, which accounts for increased cusp rounding. In most of the "mabra" species however it is not known what component of the diet causes this abrasive impact. Besides silica phytoliths, which are not restricted to monocotyledons but may also be present in dicotyle fruit and foliage (e.g. Piperno 2002), exogenous grit may have played an important role as an abrasive component. The close classification of some of the Chalicotheriinae with members of the "mabra" group may therefore shed some light on the inconsistency between mesowear and microwear signatures.

In the Schizotheriinae investigated here (*Metaschizotherium fraasi* and *Metaschizotherium* sp.) our interpretation relies on the mesowear signal only. Here we find an affinity with
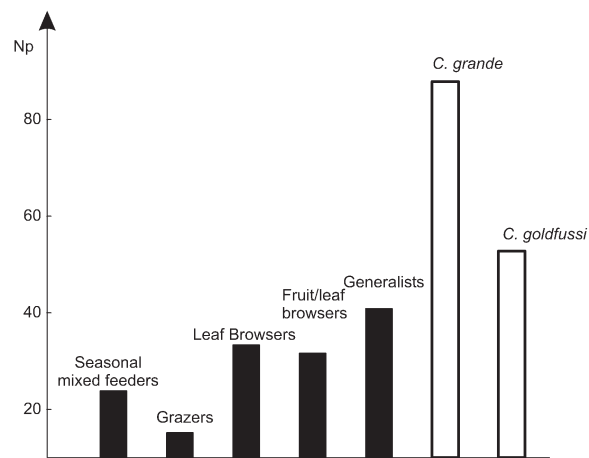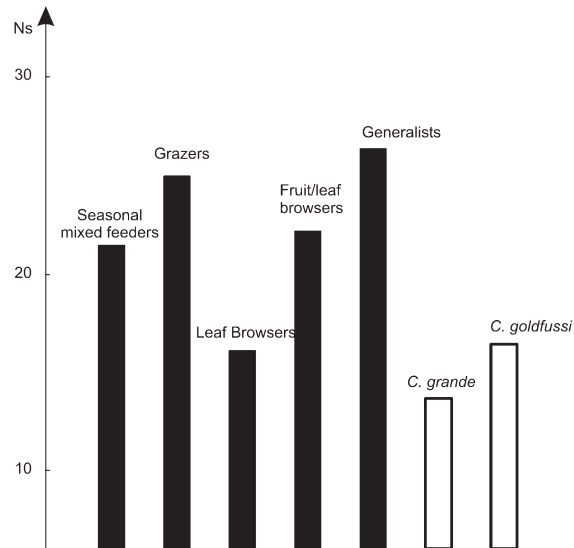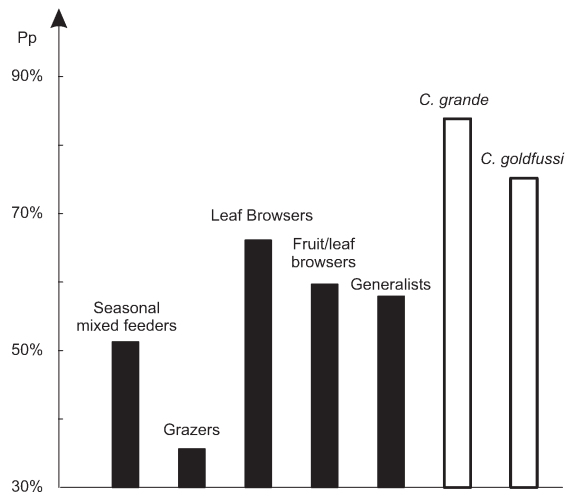
extant intermediate feeders only. As conclusion we have to reject our hypothesis 1, in general neither the Chalicotheriinae nor the Schizotheriinae investigated match the dietary trait of typical extant browsing ungulates (e.g. KOENIGSWALD 1932; ZAPFE 1976 1979; COOMBS 1982, 1989; HEISSIG 1999).

A diet composed on tough foliage and also including fibrous and hard material would be supported also by the mandibular anatomy of the Chalicotheriinae. Compared to the Schizotheriinae (cf. *Moropus elatus* MARSH, 1877; COOMBS 1978: 14), the mandibles of the Chalicotheriinae (*Chalicotherium* (*A.*) *grande* and *C. goldfussi*) are much higher (SCHAEFER & ZAPFE 1971: 162–164). This character of the Chalicotheriinae is in agreement with longer attachments of the masseter muscles and a more massive *Musculus pterygoideus medialis* (FORTELIUS 1981). This adaptation accounts for powerful masticator movements of the low crowned selenodont dentition. A massive masseter muscle is also needed to produce increased crushing forces and in functional terms is in consistence with a rounded and robust protocone of the cheek teeth, which have a large central crushing basin. In extant ruminants the development of a central crushing basin is char-
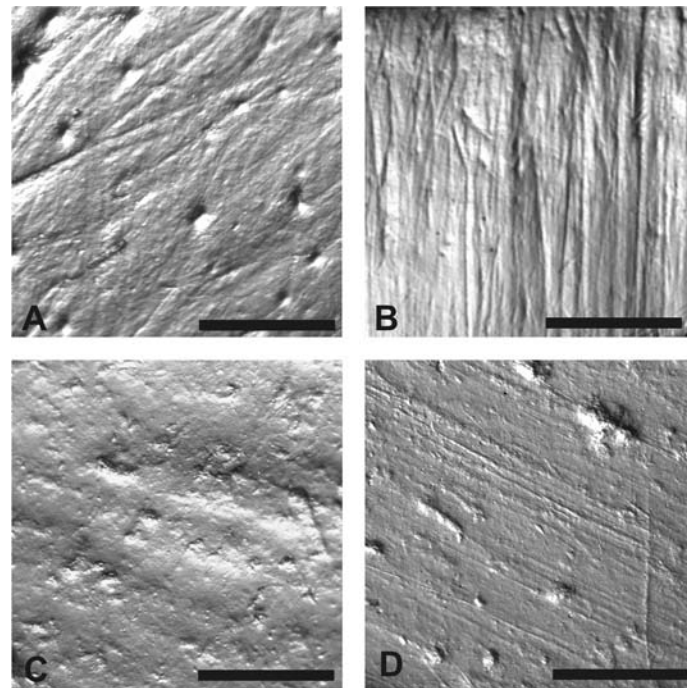


Fig. 6: Micrograph of the shearing molar facets of both, extant and extinct herbivorous mammals. A: *Diceros bicornis* (browser); B: *Equus burchelli* (grazer); C: *Chalicotherium* (*Anisodon*) *grande*; D: *Chalicotherium goldfussi*. Scale bars = 300 μm.

Fig. 5: Mean value of microwear variable. Numbers of scratches (*Ns*) and pits (*Np*), and pit percentage (*Pp*). Extant reference species from the "Ungulates" database (MERCERON et al., 2004b, 2006) are categorized following their feeding trait (black columns) and compared to the fossil taxa *Chalicotherium goldfussi* and *Chalicotherium* (*Anisodon*) *grande* (white columns).

acteristic of a browsing adaptation, because cell content is being extracted here (Archer & Sanson 2002). When taken together, these morphological features would indicate strong crushing and grinding masticatory dynamics. A similar combination of functional masticatory traits is also found in several primates, and in the Hyracoidea Huxley, 1979, furthermore it is also considered as a model for primitive ungulate dentitions (Janis 1979, 1990, 1995). In addition, the Chalicotheriinae are characterized by particularly pronounced and long shearing crests along the paracone and metacone, a character they share with extant browsing ruminants (Archer & Sanson 2002). The dentition of the Chalicotheriinae therefore appears to be functionally determined in masticating tough food items, a functional trait which appears to be even more developed as compared with extant ruminants.

## II. Does postcranial morphology reflect feeding trait (hypothesis 2)

The Chalicotheriidae are interpreted as pure browsers (Koenigswald 1932; Zapfe 1976, 1979; Coombs 1982, 1989 and Heissig 1999). Besides the brachydont dentition in both subfamilies this interpretation is based on the peculiar postcranial adaptations.

Compared to the Schizotheriinae, the hindlimbs of the Chalicotheriinae are shorter and the tarsals are proximo-distally flattened (Zapfe 1979; Coombs 1982, 1989; Schaefer & Zapfe 1971). Thus, the hindlimbs were assumed to be capable of bearing their body weight in an erected posture (e.g. Zapfe 1979; Coombs 1982, 1989; Heissig 1999). Zapfe (1979) additionally noted a specialization in the cervical vertebrae and in the shoulder joint in *Chalicotherium* (*Anisodon*) *grande* and therefore suggested an erected posture of the neck and the ability for these Chalicotheriinae to move their forelimbs upwards. A distinct *Tuber ischiadicum* is interpreted as possibly having enabled *C.* (*A.*) *grande* to rest in a sitting position (Zapfe 1979; cf. Agustí & Antón 2002). This functional reconstruction fits with the extremely elongate, slender and high ungual phalanges of the Chalicotheriinae quite well, which are a common character of this subfamily, probably bearing enormously large claws. The function of these claws was often seen in tearing down branches to reach foliage from tree canopies. A conventional position of the manus during quadrupedal locomotion is impossible for the representatives of the Chalicotheriinae, as can be deduced from the morphology of the forelimbs (e.g. Zapfe 1979; Coombs 1982, 1989; Heissig 1999).

The abrasive mesowear signal indicates a dietary trait similar to the "mabra" group of extant species for at least the *Chalicotherium* (*A.*) *grande* sub-group (MN 5–6). However, the hard items responsible for the "mabra" mesowear pattern are most likely seeds of fruit, which make up a major component of the diet of extant "mabra" species. Dental microwear however, shows high ratios of pitting in *C.* (*A.*) *grande* but no characteristic seed pits as seen in *Diceros bicornis* Linné, 1758. Since hard seeded fruit can thus be excluded as a major dietary component based on the microwear signature, an abrasive dietary component different from fruit must be considered in *C.* (*A.*) *grande*, which

however may also play a role in the diet of the "mabra" species. The "mabra" species classifying closest to the first *C. (A.) grande* sub-group (MN 5–6) is *Dendrohyrax dorsalis*. This species is a selective browser having a rather diverse diet, which besides leaves comprises abrasive components such as seeds, fruits, bark, twigs, and also grasses (GAYLAND & KERLEY 1997). Especially the bark and twigs component may be tougher as well as richer in fibres than pure leave browse would be. A substantial amount of twigs and bark would also be in accordance to ecological scenarios laid out for members of this group based on their postcranial anatomy and dental cross anatomy. The main argument for the consumption of branches and twigs is seen in the morphology of the forelimbs (e.g. ZAPFE 1979; COOMBS 1982, 1989). Considering both, postcranial morphology and wear, most likely entire twigs were consumed rather unselectively. Thus, the abrasive mesowear signal in *C. (A.) grande* from MN 8–9 and in *C. goldfussi* from MN 9 would confirm the interpretation of the anatomy of the hand. It would explain the abrasive signal seen in the diet of the Chalicotheriinae as a result of twig and bark consumption in addition to leaf browsing.

Attempts to reconstruct ecomorphological traits of the Schizotheriinae have resulted in far more divergent interpretations. Members of the Schizotheriinae were assumed to have been fossorial (e.g. ABEL 1922) and have been considered leaf-eaters feeding erected on their hindlimbs (e.g. SCHAUB 1943). COOMBS (1982, 1989) also suggests a browsing dietary trait, but postulates a less frequent use of the bipedal position when compared to the Chalicotheriinae. In her interpretation COOMBS refers to the plesiomorphic, typically perissodactyl proportion of the fore- and hindlimbs. These schizotheriine body proportions encouraged ZAPFE (1979) to state a throughout quadrupedal mode of walking. This is in accordance with the presumed mechanism of overstretching the metacarpo-phalangeal joint in order to keep the claws off the ground (cf. COOMBS 1982, 1989; SCHAUB 1943). These claws are far more robust than in the Chalicotheriinae. KOENIGSWALD (1932) considered a fossorial adaptation of *Metaschizotherium* species (Schizotheriinae) to be unlikely, because forces applied to the claws when digging would have probably caused fractures. He considered the claws of all Chalicotheriidae to have served in stripping off the bark of trees, or alternatively in opening fruit. The use of the claws as a weapon in defence (inter- and/or intraspecific) has also been taken into consideration (e.g. COOMBS 1982; KOENIGSWALD 1932; ZAPFE 1979).

In the Chalicotheriinae, our data would partly support the reconstruction by KOENIGSWALD (1932), because bark may have played a role as a source of food, while in the Schizotheriinae investigated here the claws were probably used differently, but still within the possibilities proposed by KOENIGSWALD (1932). The Schizotheriinae *M. fraasi* and *Metaschizotherium* sp. investigated are both classified as intermediate feeders. This dietary signal which accounts for less abrasive food components compared to the Chalicotheriinae would thus also be reflected by their claw morphology. We therefore tentatively regard our second hypothesis as supported, that post cranial anatomy confirms the dietary adaptation.

# E. Conclusion

It is shown that mesowear and microwear analyses shed light on complementary aspects of the palaeodiet of the Chalicotheriidae. If interpreted independently, microwear classifies the chalicotheriines as browsers while mesowear indicates a grazing or intermediate feeding regime. In combining evidence from both methods, however, the dietary signal can be accommodated with both limb and tooth morphology.

As a limiting factor in this study, we recognize the small number of dental individuals available in particular for the Schizotheriinae, which made microwear analysis of this group impossible. Further analyses including more extensive material will certainly also allow temporally better resolved assessments of the ecological role of the Chalicotheriidae in the Miocene palaeoenvironments of Central Europe.

# F. Acknowledgements

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climatol., Palaeoecol., *186*: 145–161.

Appendix 1. List of fossil specimens investigated by means of mesowear and microwear analyses.

| specimen | species | locality | MN unit | molded teeth | mesowear | microwear |
|---|---|---|---|---|---|---|
| HLMD-DIN3171 (sin.) | Chalicotherium goldfussi | Bermersheim near Alzey | MN9 | $M_3$ | | x |
| HLMD-Din3139 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^1$ | x | x |
| HLMD-Din3168 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^1$ | x | |
| HLMD-Din3141 (dext.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^2$ | x | x |
| HLMD-Din3168 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^2$ | x | |
| HLMD-Din3124 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^3$ | x | x |
| HLMD-DIN3140 (dext.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M_3$ | | x |
| HLMD-Din3167 (dext.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^3$ | x | x |
| HLMD-Din3168 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $M^3$ | x | |
| HLMD-Din3168 (sin.) | Chalicotherium goldfussi | Eppelsheim | MN9 | $P^4$ | x | |
| HLMD-DIN3142 (sin.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M_1$ or $M_2$ or $M_3$ | x | x |
| HLMD-Din3116 (sin.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M^2$ | x | x |
| HLMD-Din3126 (dext.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M^2$ | x | |
| HLMD-Din3130 (dext.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M^2$ | x | |
| HLMD-DIN3143 (dext.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M_3$ | | x |
| HLMDDIN3166 (dext.) | Chalicotherium goldfussi | Esselsborn | MN9 | $M_3$ | | x |
| HLMD-Din1898 (dext.) | Chalicotherium goldfussi | Esselsborn | MN9 | $P^4$ | x | |
| HLMD-DIN3132 (dext.) | Chalicotherium goldfussi | Gauweinheim | MN9 | $M_2$ | | x |
| BSP-1956I518 (dext.) | Chalicotherium goldfussi | Gauweinheim | MN9 | $M_3$ | | x |
| HLMD-Din3119 (sin.) | Chalicotherium goldfussi | Gauweinheim | MN9 | $M^3$ | x | x |
| HLMD-DIN3135 (dext.) | Chalicotherium goldfussi | Gauweinheim | MN9 | $M_3$ | | x |
| BSP-1959XIII13 (sin.) | Chalicotherium goldfussi | Westhofen | MN9 | $M^3$ | | x |
| BSP-1959XIII14 (dext.) | Chalicotherium goldfussi | Westhofen | MN9 | $P_4$ | x | x |
| BSP-1956I516 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^1$ | x | x |
| BSP-1956I517 (dext.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^1$ | x | x |
| HLMD-Din3127 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^1$ | x | |
| HLMD-Din3128 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^1$ | x | |
| BSP-1955I329 (dext.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^2$ | | x |
| BSP-1956I514 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^2$ | x | x |
| BSP-1956I519 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M_2$ | | x |
| BSP-1956I515 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^3$ | x | |
| HLMD-Din3129 (sin.) | Chalicotherium goldfussi | Wissberg near Gauweinheim | MN9 | $M^3$ | x | |
| HLMD-Din3120 (dext.) | Chalicotherium goldfussi | Wolfsheim | MN9 | $M^2$ | x | |

| specimen | species | locality | MN unit | molded teeth | mesowear | microwear |
|---|---|---|---|---|---|---|
| NMA2005/183–1927 (sin.) | *Chalicotherium (Anisodon) grande* | Burg-Balzhausen (Wand) | MN56 | $P^4$ | x | |
| NMA451/1361 (dext.) | *Chalicotherium (Anisodon) grande* | Derching near Augsburg | MN6 | $M^3$ | x | |
| BSP-1962I193 (dext.) | *Chalicotherium (Anisodon) grande* | Friedberg near Augsburg | MN6 | $M^1$ | | x |
| NMA2005/184/1633 (sin.) | *Chalicotherium (Anisodon) grande* | Hohenraunau | MN56 | $M^3$ | x | |
| NMA 2005/182/1415 (dext.) | *Chalicotherium (Anisodon) grande* | Kirrberg, Tongrube | MN6 | $M^2$ | x | |
| BSP-1934I24 (dext.) | *Chalicotherium (Anisodon) grande* | Lochhausen | MN89 | $M^1$ | x | x |
| BSP-1934I24 (dext.) | *Chalicotherium (Anisodon) grande* | Lochhausen | MN89 | $M^3$ | x | |
| BSP-1934I24 (dext.) | *Chalicotherium (Anisodon) grande* | Lochhausen | MN89 | $P^4$ | x | |
| BSP-1957I189 (dext.) | *Chalicotherium (Anisodon) grande* | Massenhausen near Freising | MN8 | $M_3$ | | x |
| BSP-1957I434 (sin.) | *Chalicotherium (Anisodon) grande* | Massenhausen near Freising | MN9 | $M^3$ | x | x |
| BSP-1957VII54 (dext.) | *Chalicotherium (Anisodon) grande* | Redertshausen | MN6 | $M^3$ | x | x |
| BSP-1971I187 (sin.) | *Chalicotherium (Anisodon) grande* | Thannhausen | MN6 | $M^1$ | x | x |
| BSP-1968I179 (sin.) | *Chalicotherium (Anisodon) grande* | Thannhausen, Gärtnerei Geisselmann | MN6 | $M^1$ | x | x |
| BSP-1968I180 (sin.) | *Chalicotherium (Anisodon) grande* | Thannhausen, Gärtnerei Geisselmann | MN6 | $M^1$ | x | x |
| BSP-1975I27 (sin.) | *Chalicotherium (Anisodon) grande* | Thannhausen, Gärtnerei Geisselmann | MN6 | $M_3$ | | x |
| BSP-150I68 (sin.) | *Chalicotherium (Anisodon) grande* | Wartenberg | MN89 | $M^2$ | x | x |
| BSP-1985XIV143 (sin.) | *Chalicotherium (Anisodon) grande* | Zahling | MN6 | $M^1$ | x | |
| BSP-1985XIV143 (sin.) | *Chalicotherium (Anisodon) grande* | Zahling | MN6 | $M^2$ | x | x |
| BSP-1985XIV143 (sin.) | *Chalicotherium (Anisodon) grande* | Zahling | MN6 | $P^4$ | x | |
| BSP-1959II11630 (dext.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^1$ | x | |
| BSP-1959II2507 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^1$ | x | |
| BSP-1959II11571 (dext.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ | x | |
| BSP-1959II11612 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ | x | |
| BSP-1959II11621 (dext.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ | x | |
| BSP-1959II11624 (dext.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ | x | |
| BSP-1959II2507 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ | x | |
| BSP-1959II11614 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^2$ or $M^3$ | x | |
| BSP-1959II2507 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $M^3$ | x | |
| BSP-1959II11573 (dext.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $P^4$ | x | |
| BSP-1959II2507 (sin.) | *Metaschizotherium sp.* | Sandelzhausen | MN5 | $P^4$ | x | |
| MR2/71–1 (dext.) | *Metaschizotherium fraasi* | Petersbuch | MN6 | $M^2$ | x | |
| MR2/71–2 (dext.) | *Metaschizotherium fraasi* | Petersbuch | MN6 | $P^4$ | x | |
| MR2/71–3 (sin.) | *Metaschizotherium fraasi* | Petersbuch | MN6 | $P^4$ | x | |
| MR2/71-H-1 (dext.) | *Metaschizotherium fraasi* | Petersbuch | MN6 | $P^4$ | x | |

Appendix 2: Database after FORTELIUS & SOLOUNIAS (2000), modified by KAISER & SOLOUNIAS (2003). List of species with number of specimens categorized by their diet following the classification by FORTELIUS & SOLOUNIAS. For further information regarding specimen provenance, see FORTELIUS & SOLOUNIAS (2000). * = "no particular class" and $^{M}$ = "minute abraded" feeding species (cf. FORTELIUS & SOLOUNIAS 2000)

| intermediate feeders | N | browsers | N | grazers | N |
|---|---|---|---|---|---|
| Aepyceros melampus | 17 | Alces alces | 30 | Alcelaphus buselaphus | 76 |
| Antidorcas marsupialis* | 26 | Ammodorcas clarkei* | 7 | Alelaphus lichtensteinii* | 17 |
| Axis axis* | 43 | Antilocapra americana* | 44 | Bison bison | 15 |
| Axis porcinus* | 24 | Capreolus capreolus* | 68 | Ceratotherium simum | 26 |
| Boselaphus tragocamelus* | 15 | Cephalophus dorsalis$^{M}$ | 28 | Connochaetes taurinus | 52 |
| Budorcas taxicolor* | 38 | Cephalophus natalensis$^{M}$ | 6 | Damaliscus lunatus | 5 |
| Capra ibex* | 24 | Cephalophus niger$^{M}$ | 31 | Equus burchelli | 122 |
| Capricornis sumatraensis | 22 | Cephalophus nigrifrons$^{M}$ | 44 | Equus grevyi | 29 |
| Cervus canadensis | 19 | Cephalophus silviculor$^{M}$ | 39 | Hippotragus equinus | 26 |
| Cervus duvauceli* | 50 | Dendrohyrax arboreus$^{M}$ | 20 | Hippotragus niger | 20 |
| Cervus unicolor* | 21 | Dendrohyrax dorsalis$^{M}$ | 28 | Kobus ellipsiprymnus | 22 |
| Gazella granti | 18 | Dicerorhinus sumatraensis | 5 | Redunca redunca | 77 |
| Gazella thomsoni | 146 | Diceros bicornis | 34 | | |
| Ourebia ourebi* | 128 | Giraffa camelopardalis | 61 | | |
| Ovibos canadensis* | 31 | Heterohyrax brucei$^{M}$ | 11 | | |
| Ovibos moschatus | 52 | Hyemoschus aquaticus$^{M}$ | 18 | | |
| Procavia capensis$^{M}$ | 24 | Litocranius walleri* | 69 | | |
| Redunca fulvorufula* | 7 | Odocoileus hemionus | 33 | | |
| Rhinoceros unicornis* | 5 | Odocoileus virginianus | 18 | | |
| Saiga tatarica* | 5 | Okapia johnstoni | 8 | | |
| Syncerus caffer* | 31 | Rhinoceros sondaicus | 5 | | |
| Taurotragus oryx | 14 | Tragelaphus euryceros* | 27 | | |
| Tetracerus quadricornis* | 21 | Tragelaphus strepsiceros* | 7 | | |
| Tragelaphus angasi* | 20 | | | | |
| Tragelaphus imperbis* | 31 | | | | |
| Tragelaphus scriptus | 47 | | | | |
| Σ 879 | | Σ 641 | | Σ 487 | |
| | | | | Σ 2007 | |

Appendix 3: The "Ungulate" database (Muséum d'Histoire Naturelle Paris, Office National de la Chasse et de la Faune Sauvage – Centre Nationale de la Recherche Scientifique Chizé, Institut de Recherche sur les Grands Mammifères – Institut National de la Recherche Agronomique Toulouse, France; Senckenberg Naturmuseum Frankfurt, Staatliches Museum für Naturkunde, Stuttgart, Germany).

| feeding group | species | N |
|---|---|---|
| Grazers | *Alcelaphus buselaphus* | 28 |
| | *Damaliscus lunatus* | 14 |
| | *Equus burchelli* | 24 |
| | *Equus przewalskii* | 6 |
| | *Hippotragus niger* | 13 |
| | *Kobus kob* | 26 |
| | *Ourebia ourebi* | 18 |
| | *Redunca redunca* | 5 |
| | *Syncerus cafer* | 24 |
| Seasonal mixed feeders | *Aepyceros melampus* | 19 |
| | *Taurotragus oryx* | 4 |
| | *Tragelaphus scriptus* | 18 |
| Traditional browsers | *Diceros bicornis* | 10 |
| | *Giraffa camelopardalis* | 16 |
| | *Litocranius walleri* | 16 |
| | *Sylvicapra grimmia* | 24 |
| | *Tragelaphus euryceros* | 4 |
| | *Tragelaphus strepsiceros* | 8 |
| Fruit browsers | *Capreolus capreolus* | 128 |
| | *Cephalophus* sp.[1] | 14 |
| | *Odocoileus virginianus* | 11 |
| | *Mazama americana* | 6 |
| | *Muntiacus muntjak* | 8 |
| Generalists | *Cervus elaphus* | 47 |
| | *Ovibos moschatus* | 8 |
| | *Ovis ammon* | 9 |
| | *Rangifer tarandus* | 17 |
| | *Rupicapra* sp.[2] | 21 |
| | Σ | **546** |

[1] *Cephalophus* sample (*C. sylvicultor* N = 8; *C. dorsalis* N = 1; *C. leucogaster* N = 3; *C. callypigus* N = 2)
[2] *Rupicapra* sample (*R. pyrenaica* N = 16; *R. rupicapra* N = 5).