

# *Anisodon* sp. (Mammalia, Perissodactyla, Chalicotheriidae) from the Turolian of Dorn-Dürkheim 1 (Rheinhessen, Germany): morphology, phylogeny, and palaeoecology of the latest chalicothere in Central Europe

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**Abstract** The rich mammalian fauna of the Turolian fossil site Dorn-Dürkheim 1 (Rheinhessen, Rheinland-Pfalz, Germany) contains numerous remains of a chalicotheriine chalicothere. These are 171 dental remains, 1 fragment of a lower jaw symphysis, and 8 carpal and tarsal bones. A morphological description and comprehensive comparison with other Eurasian Chalicotheriinae are given. The Dorn-Dürkheim 1 chalicothere was comparatively small in body size and resembled members of the *Anisodon* clade rather than *Chalicotherium* within the Chalicotheriinae. A phylogenetic analysis corroborates the assignment of the Dorn-Dürkheim 1 chalicothere to *Anisodon* sp. We used low-magnification stereoscopic microwear analysis in order to reconstruct the diet of *Anisodon* sp. from Dorn-Dürkheim 1.

Counts of small pits are higher than in earlier Eurasian and American chalicotheres. *Anisodon* sp. from Dorn-Dürkheim 1 most likely fed on leaves and fruit. There is no indication of the inclusion of highly abrasive material, grit, or dust in its diet. These results are in accordance with the interpretation of the Dorn-Dürkheim 1 environment as a tropical savannah woodland. The dating of the Dorn-Dürkheim 1 fauna as Mammal Neogene (MN) 11 makes this *Anisodon* the latest known chalicothere in Central Europe. Based on morphological similarities with late Miocene chalicotheriines from Asia and southeastern Europe, we assume that it is an immigrant that arrived in the course of the expansion of faunas from the southeast at the beginning of the Turolian.

**Keywords** Chalicotheriinae · *Anisodon* · Microwear · Palaeoecology · MN 11 · Faunal turnover

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## Introduction

### General information

Chalicotheres are a group of perissodactyls known for their curious, sloth-like morphology (“Pangolin gigantesque”; Cuvier 1823), especially with regard to the large claws that grace their hands and feet instead of hooves. The Chalicotherioidea include several basal taxa such as *Litolophus* and *Eomoropus*, and the monophyletic Chalicotheriidae, and were distributed in North America, Eurasia, and Africa from Eocene through Pleistocene times (Coombs 1989, 1998).

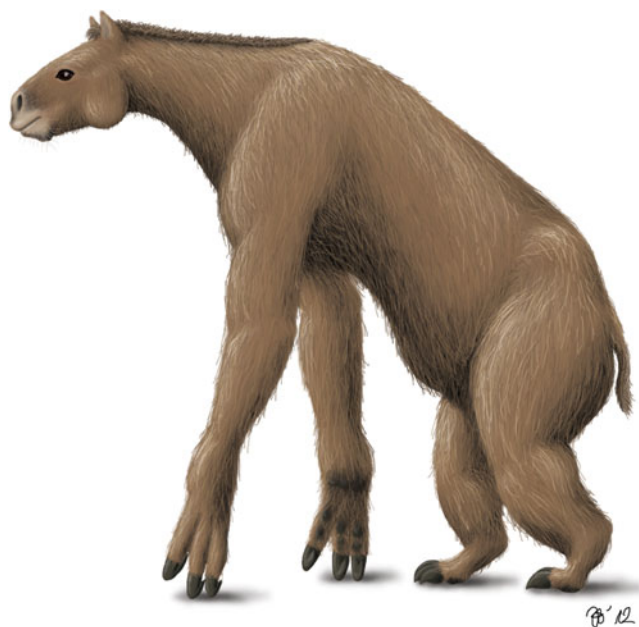
From the Oligocene onward, two subfamilies are recognised within the Chalicotheriidae: the Chalicotheriinae

and the Schizotheriinae, which are readily distinguishable based on morphological characters. Retaining low-crowned and square molars, the Chalicotheriinae show strong modifications of the postcranium, e.g. shortening of zeugopodial and autopodial bones of the hind limb, loss of metacarpal V, and lateral compression of the ungual phalanges. In contrast, the Schizotheriinae retained less dramatically specialised body proportions, but show an evolutionary trend from low to higher crowned and to more elongated molars (Coombs 1989, 1998). A life-like reconstruction of a chalicotheriine chalicothere, based on the skeletal reconstruction of *Anisodon grande* by Zapfe (1979), is given in Fig. 1.

Based on mesowear and microwear analyses, Chalicotheriidae have been reconstructed as fruit and/or leaf browsers with varying amounts of abrasive components in their diet (Schulz et al. 2007; Schulz and Fahlke 2009; Semprebon et al. 2009, 2011). Leaf browsing with possible bark ingestion, sometimes combined with obvious grit ingestion, was apparently more common in Miocene or younger schizotheriines from America and Eurasia, whereas fruit browsing and seed ingestion was likely in most Eocene and Oligocene chalicotheriids, in some European Miocene schizotheriines, and in Miocene chalicotheriines. The latter seem to have fed on the most resistant food (Semprebon et al. 2011).

#### Chalicotheriine phylogeny and taxonomy

The complexity of chalicotheriine evolution was neglected for many decades. It was long assumed that large late Miocene



**Fig. 1** Reconstruction of a chalicotheriine chalicothere of the *Anisodon* clade, based on the skeletal reconstruction of *A. grande* by Zapfe (1979, fig. 155)

forms such as *Chalicotherium goldfussi* ascended from smaller middle Miocene forms such as “*Chalicotherium*” *grande* in Central Europe (Butler 1965; Heissig 1999; Zapfe 1979). Within the past two decades, however, chalicotheriine phylogeny and taxonomy have been revised (Anquetin et al. 2007; Chen et al. 2012; de Bonis et al. 1995; Geraads et al. 2001). The existence of two derived chalicotheriine clades, the *Anisodon* clade, including *Nestoritherium*, and the *Chalicotherium* clade, is now commonly accepted. These analyses have placed the early Miocene species *Butleria rusingensis* in a relatively basal position within the Chalicotheriinae.

#### Anatomical abbreviations

c, lower canine; dext., dextral; DP, upper deciduous premolar; dp, lower deciduous premolar; di, lower deciduous incisor; i, lower incisor; M, upper molar; m, lower molar; Mc, metacarpal; Mt, metatarsal; P, upper premolar; p, lower premolar; sin., sinistral.

#### Institutional abbreviations

AM, Assenovgrad Museum, Assenovgrad, Bulgaria; AMNH, American Museum of Natural History, New York, USA; BMNH British Museum Natural History, London, UK; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CCECM, Centre de Conservation et d’Étude des Collections du Muséum, Lyon, France; DD, Dorn-Dürkheim 1 collection of the Senckenberg Museum Frankfurt am Main, Germany; HLMD, Hessisches Landesmuseum Darmstadt, Germany; HVM, Hezheng Paleozoological Museum, Gansu, China; IPMC, Institut Paleontològic Dr. M. Crusafont, Sabadell, Spain; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KNM, Kenya National Museum, Nairobi, Kenya; LGPUT, Laboratory of Geology and Palaeontology, Aristotelian University of Thessaloniki, Greece; LMJ, Landesmuseum Joanneum Graz, Austria; MHNT, Muséum d’Histoire Naturelle, Toulouse, France; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MTA, General Directorate of Mineral Research and Exploration, Ankara, Turkey; NHMM-LS, Naturhistorisches Museum/Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany; NHMW, Naturhistorisches Museum Wien, Austria; NMA, Naturmuseum Augsburg, Germany; NMB, Naturhistorisches Museum Basel, Switzerland; PMS, Prirodonamen Muzej Skopje, Macedonia; SMF, Senckenberg Museum Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; UA, Department of Historical Geology and Paleontology, University of Athens, Greece; XBDD, Northwest University Geological Department, Xian, Shaanxi, China.

## Materials and methods

### Material and measurements

The fossil chalicothere material from Dorn-Dürkheim 1 comprises 171 isolated permanent and deciduous teeth and tooth fragments of almost all tooth positions as well as 1 lower jaw symphysis, and 8 bones of the autopodium. Preservation of the teeth is generally good, while most of the bones are severely damaged.

The material was examined, and measurements were taken with standard calipers to a precision of 0.1 mm. Elements and measurements are listed in Online Resource 1.

The minimum individual number (MNI) was calculated based on the maximum number of teeth of the same tooth position from the same body side.

### Comparative material

In order to assign the Dorn-Dürkheim 1 material taxonomically, we compared it to other known Chalicotheriinae from the Miocene to Pleistocene. Much of the comparative material has been examined by either J.M.F. or M.C.C., or both, at various collections. Where no personal inspection of the material was possible, the comparison is based on the literature. Comparative material used in this study and respective references are given in Table 1.

### Phylogenetic analysis

The phylogenetic analysis conducted in this study is based on the character description and coding used in Anquetin et al. (2007), who in turn referred to and thoroughly discussed characters used by de Bonis et al. (1995).

Due to the lack of cranial remains other than teeth from Dorn-Dürkheim 1, we only used mandibular and dental characters (characters 33–51 of Anquetin et al. 2007). Of these, character 50 (trigonid of the lower molars U-shaped or V-shaped) was also omitted due to high intraspecific variability and therefore low significance of this character in phylogenetic analyses (see “Discussion”). Altogether, 18 characters were used.

Furthermore, we re-coded several characters of Anquetin et al. (2007) for *A. grande*, *A. sivalense*, *C. goldfussi*, and *C. brevirostris*, based on our own findings, recent literature (see Table 1), and the inclusion of additional material.

In our analysis, the basal chalicothere *Eomoropus* served as the outgroup. Including the material from Dorn-Dürkheim 1, 12 chalicotheriines and the schizotheriine *Moropus* were included in the analysis. *Hesperotherium sinense* and *Nestoritherium linxiaense* were included using the character codings by Chen et al. (2012). *A. wuduensis* and *Anisodon* sp. from Titov Veles, which are based on lower jaws that

Anquetin et al. (2007) included in their study, were excluded from this phylogenetic analysis due to an insufficient number of characters from the chosen character set that could be scored (6 out of 18 each). Additional comparative materials considered in the discussion were also omitted from the analysis for the same reason. The matrix and a character list, including references to the original character numbering by Anquetin et al. (2007), are given in Online Resource 2. Analyses were run in T.N.T. 1.1 and Mesquite 2.75. All characters were treated as unordered.

The purpose of our analysis was to suggest, as closely as possible, the phylogenetic placement of *Anisodon* sp. from Dorn-Dürkheim 1 within the Chalicotheriinae. For this reason, we do not suggest any changes in taxonomic assignment based on our limited dataset and use the generic assignments proposed by Anquetin et al. (2007) and in some cases by Chen et al. (2012) throughout our comparisons and discussion.

### Microwear analysis

We quantified wear features on the enamel of shearing facets on upper and lower second molars using low-magnification stereoscopic microwear analysis after Solounias and Semprebon (2002). When possible, the buccal cusps on upper and lower second molars were sampled. Due to the small sample size, upper and lower first molars were equally sampled, so that a sample size of  $n=12$  was reached.

Enamel surfaces of the chalicothere teeth from Dorn-Dürkheim 1 were cleaned with acetone-drenched soft cotton pads. Teeth were moulded using Heraeus Kulzer Provil<sup>®</sup> novo Light regular set and Putty regular set. Casts were made using Buehler EpoKwick clear epoxy resin. Enamel surfaces were then analysed using a Zeiss Stemi-2000C stereoscopic microscope and a M1-150 High Intensity fiber optic light source (Dolan-Jenner).

Wear features were counted by G.M.S. in a  $0.4 \times 0.4$  mm square area at a magnification of  $\times 35$  directly on the casts following the protocol developed by Solounias and Semprebon (2002) and tested by Semprebon et al. (2004). We counted small and large pits and distinguished puncture-like pits of various sizes. Large puncture pits have diameters of 0.1 mm or larger, small puncture pits have diameters of 0.03 mm or smaller, and medium puncture pits have diameters falling in between those of small and large puncture pits. The presence or absence of gouges was also noted. We also counted scratches and categorised scratch textures as being predominantly fine (f), coarse (c), a mixture of fine and coarse (m), hypercoarse (h), or a mixture of coarse and hypercoarse (ch). Two counts per tooth were made where possible and averages for individuals were calculated. A list of the sampled Dorn-Dürkheim 1 specimens and the average microwear counts are given in Table 2.

**Table 1** Miocene to Pleistocene Chalicotheriinae used in comparisons in this paper

Genus/species	Main localities	Age	Collections	Material	Seen by	Important references
<i>Chalicotherium goldfussi</i>	Dinothiersandte at Eppelsheim (and vicinity), Germany	MN 9	HLM, SMF, SMNK, NHMM-LS	D, C, P	JMF, MCC	Kaup (1833), Anquetin et al. (2007)
<i>Chalicotherium goldfussi</i>	Höwenegg, Germany	MN 9	SMNK	D	JMF	Anquetin et al. (2007)
<i>Chalicotherium goldfussi</i>	Atzelsdorf, Austria	MN 9	NHMW	D, P	JMF	Heissig (2009)
<i>Chalicotherium goldfussi</i>	Gaiselberg, Austria	MN 9	NHMW	D, P	JMF	Zapfe (1949a, b, 1979)
<i>Chalicotherium goldfussi</i>	Saint-Gaudens, France	MN 8	MHNT	D, C	MCC	de Bonis et al. (1995), Anquetin et al. (2007)
<i>Chalicotherium goldfussi</i>	La-Grive-St. Alban, France	MN 7–8	CCECM, AMNH (cast)	D, C	MCC	Depéret (1892), de Bonis et al. (1995), Anquetin et al. (2007)
? <i>Chalicotherium goldfussi</i>	Nikolsburg (= Mikulov), Czech Republic	MN 9	NHMW, AMNH (cast), BSPG	D, C	JMF, MCC	Abel (1922)
? <i>Chalicotherium goldfussi</i>	Hostalats de Pièrola (upper level) and other upper Miocene sites, Spain	MN 9–10	IPMC	D		Villalta and Crusafont (1945), Cerdèño and Alberdi (2006)
<i>Chalicotherium sylvaticum</i>	Eggersdorf, Austria	MN 9	LMJ	D, C	MCC	Bach (1912), Butler (1965), Mottl (1970), de Bonis et al. (1995)
? <i>Chalicotherium baltavensis</i>	Baltavar, Hungary	MN 13	BMNH (cast)	D, C		Pethő (1885), Butler (1965)
<i>Chalicotherium brevisrostris</i>	Tunggur, Inner Mongolia, China	MN 7–8	AMNH, IVPP	D, C	JMF, MCC	Colbert (1934), Liu and Zhang (2012)
<i>Kalimansia bulgarica</i>	Kalimantsi-Pehtsata, Bulgaria	MN 11/12?	AM	D, C		Geraards et al. (2001), Anquetin et al. (2007)
<i>Chalicotherium</i> ? sp.	Hadjidimovo-1, Bulgaria	MN 12	AM	P		Geraards et al. (2001)
<i>Anisodon grande</i>	Sansan, France	MN 6	MNHN	D, C, P	MCC	Lartet (1851), Filhol (1891), Butler (1965), de Bonis et al. (1995), Geraards et al. (2001), Anquetin et al. (2007)
<i>Anisodon grande</i>	Neudorf, Slovakia	MN 6	NHMW, NMB	D, C, P	JMF, MCC	Zapfe (1979)
<i>Anisodon grande</i>	Thannhausen, Redershausen, and other Upper Freshwater Molasse localities, Germany	MN 6	BSPG, NMA	D	JMF, MCC	Semprebon et al. (2011)
<i>Anisodon grande</i> and/or <i>Anisodon</i> sp.	Hostalats de Pièrola (lower level) and other mid-late Miocene sites, Spain	MN 6–MN12	IPMC and others	D		Villalta and Crusafont (1945), Cerdèño and Alberdi (2006)
<i>Anisodon salinus</i>	Chinji/Nagri, Siwaliks, Pakistan	MN 8–11	BMNH, AMNH	D, C, P	JMF, MCC	Forster-Cooper (1922), Colbert 1935, Pickford (1982)
<i>Anisodon macedonicus</i>	Dytiko 3, Greece	MN 13	LGPUT, AMNH (cast)	D, C, P	JMF, MCC	de Bonis et al. (1995), Geraards et al. (2001), Anquetin et al. (2007)
<i>Anisodon macedonicus</i>	Chomatari (near Pikermi), Greece	MN 12–13	UA	D, C		Symeonidis (1973), de Bonis et al. (1995)
<i>Anisodon</i> sp.	Vathyakkos, Greece	MN 11	MNHN	D, C, P		Arambourg and Piveteau (1929), de Bonis et al. (1995), Anquetin et al. (2007)
<i>Anisodont chalicotherine</i>	Akkasdaği, Turkey	MN ~11–13	MTA	D, C		Sarac and Sen (2005)
<i>Anisodon</i> sp.	Hemendorf, Austria	MN 12–13	NHMW	D, C	JMF, MCC	Schaefer and Zapfe (1971), Anquetin et al. (2007)
<i>Anisodon</i> sp.	Titov Veles, Macedonia	MN 12	PMS	D, C		Garewski and Zapfe (1983), Anquetin et al. (2007)
<i>Anisodon wudensis</i> / <i>Nestoritherium wudensis</i>	Longjiagou, Wudu County, Gansu Province, China	MN 13	XBDD	D, C	MCC	Xue and Coombs (1985), Anquetin et al. (2007) Chen et al. (2012)
<i>Nestoritherium linxiaense</i>	Houshan and Guonigou, Liushu Formation, Linxia Basin, Gansu, China	MN 10	HMV, IVPP	D, C		Chen et al. (2012)
<i>Nestoritherium sivalense</i> / <i>Anisodon sivalense</i>	Upper Siwaliks, Pakistan	Early Pleistocene	BMNH	D, C	MCC (AMNH cast)	Colbert (1935), Anquetin et al. (2007), Chen et al. (2012)
<i>Hesperotherium sinense</i> (derived anisodont)	Nihowan fauna, Tianzhen County, Shanxi Province, and other localities, China	Late Plio- to mid Pleistocene	BMNH, IVPP	D, C		Owen (1870), Colbert and Hooijer (1953), Qiu (2002), Chen et al. (2012)
<i>Butleria rusingensis</i>	Rusinga, Mfangano, Songhor, and other sites, Kenya	MN ~3/4 equiv.	BMNH, KNM	D, C, P	MCC (BMNH)	Butler (1965), de Bonis et al. (1995), Anquetin et al. (2007), Coombs and Cote (2010)

JMF Julia M. Fahlke, MCC Margery C. Coombs, D dental, C cranial (including maxillary and mandibular fragments), P postcranial. For institutional abbreviations, see text

**Table 2** Counts of microwear features on upper and lower first and second molars of *Anisodon* sp. from Dorn-Dürkheim 1 (×3.5, 0.4×0.4 mm square) by category, and total averages thereof

Specimen number	Tooth position	Average small pits	Average large pits	Total pits	Average scratches	Gouges	Scratch texture	Average large-sized puncture pits	Average medium-sized puncture pits	Average small-sized puncture pits
DD 272	m2 sin.	67	6	73	12	No	Mixed fine and coarse	0	0	0
DD 5803	m2 dext.	54.5	5	60	8.5	No	Fine	0	0	0
DD 302	m2 (?) dext.	66.5	5.5	73	7.5	Yes	Coarse and hyper-coarse	0	0	0
DD 449	M1 dext.	49	6	55	10	Yes	Mixed fine and coarse	0	1.5	0
DD 468	m2 dext.	59.5	9	69	13	No	Coarse	0	0	9
DD 294	M1 sin.	53.5	7.5	61	16.5	No	Coarse and hyper-coarse	0	0.5	0
DD 467	m1 sin.	64	11.5	76	9.5	Yes	Coarse and hyper-coarse	0	0	11.5
DD 4699	m1 dext.	69	14.5	84	20	Yes	Coarse and hyper-coarse	0	0.5	14.5
DD 4784	m1 sin.	58	16	74	11	No	Coarse and hyper-coarse	0	0	15
DD 308	m1 sin.	56.5	12.5	70	17	No	Coarse and hyper-coarse	0	0	11.5
DD 264	m1 dext.	63	14	77	11	No	Coarse and hyper-coarse	0	1	14
DD 3872	m1 sin.	47.5	6.5	55	10.5	No	Coarse and hyper-coarse	0	0	0
	Average total	59	9.5	68.9	12.2			0	0.29	6.29

Results were compared with microwear data for other chalicotheres (Semprebón et al. 2011) and to those of various other living ungulates (database by Solounias and Semprebón 2002).

**Systematic palaeontology**

Order Perissodactyla Owen, 1848  
 Superfamily Chalicotheroidea Gill, 1872  
 Family Chalicotheriidae Gill, 1872  
 Subfamily Chalicotheriinae Gill, 1872  
 Genus *Anisodon* Lartet, 1851

*Anisodon* sp.

Description and comparison

Calculation of MNI indicates that the material of *Anisodon* sp. from Dorn-Dürkheim 1 belongs to at least nine adult and four juvenile individuals.

*Upper molars*

Molars of chalicotheriines are low-crowned. The upper molars have approximately square proportions in occlusal view. The ectoloph is W-shaped and inclined toward the buccal side. M1 is generally much smaller than M2 and 3. On the M3, the parastyle is usually positioned more anteriorly and buccally. A diagrammatic overview of upper molar morphology is given in Fig. 2a.

The upper molars of *Anisodon* sp. from Dorn-Dürkheim 1 (Fig. 2c–e) are rather roundish in outline, resembling those of *A. macedonicus*, *Anisodon* sp. from Vathylakkos, *A. grande*, and *Butleria rusingensis*.

On the upper molars, the protocone of *Anisodon* sp. from Dorn-Dürkheim 1 is positioned somewhat posterior to the paracone, as is the case in most other Chalicotheriinae (character 9; Anquetin et al. 2007, character 41). The protocone of *Anisodon* sp. from Dorn-Dürkheim 1 also projects moderately far lingually, as is seen in the chalicothere from Akkaşdağı (Turkey), the chalicothere from Nikolsburg, *A. grande*, *Anisodon* sp. from Vathylakkos, and *B. rusingensis*.

The central valley of the upper molars in *Anisodon* sp. from Dorn-Dürkheim 1 is wider than in *A. grande* and narrower than in *C. goldfussi*, as is the gap between the protocone and the hypocone.

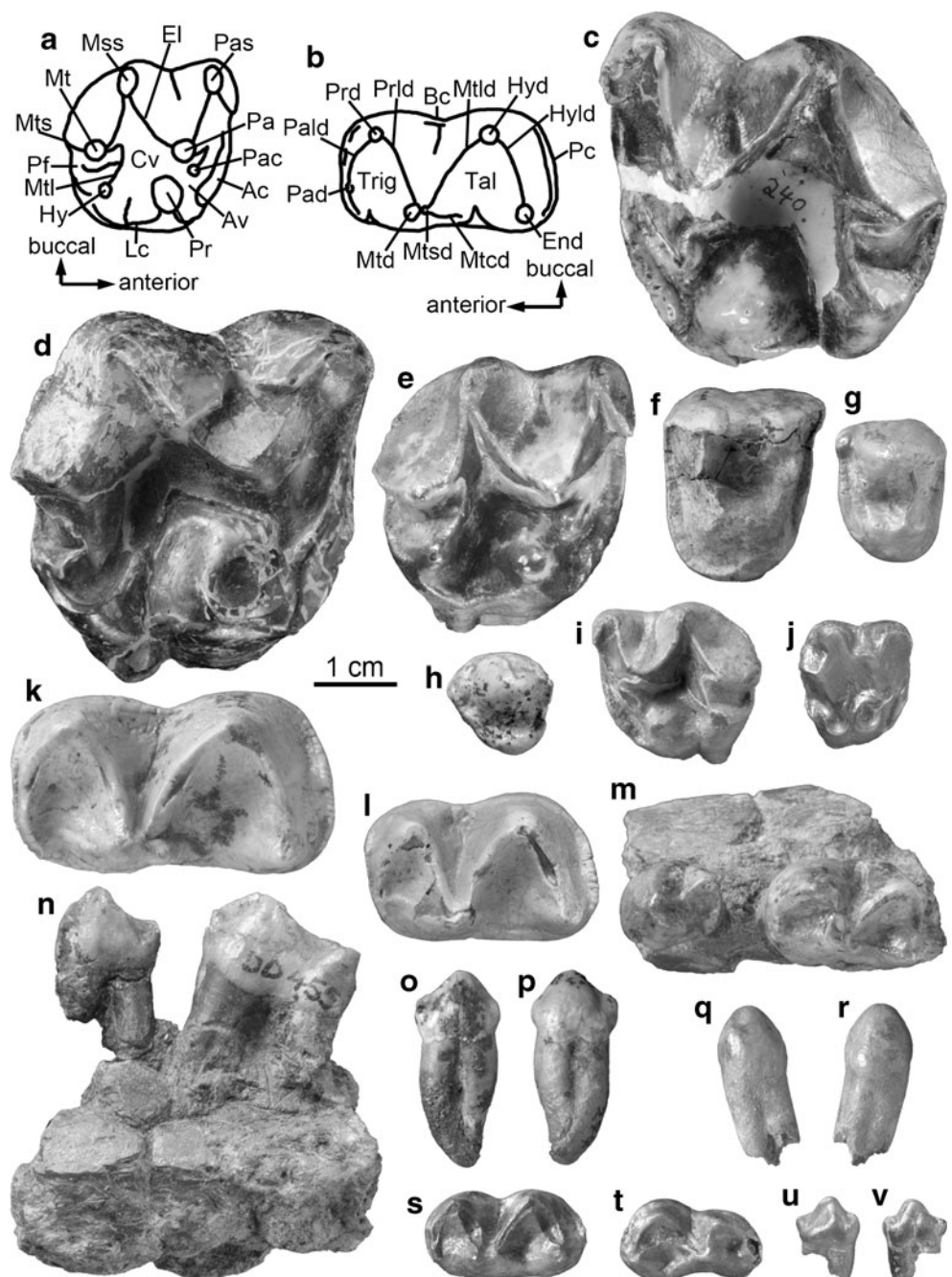
*Anisodon* sp. from Dorn-Dürkheim 1 shows no or only a weak buccal cingulum on the upper molars, thus again differing from *C. goldfussi* and resembling *A. grande*, *Anisodon* sp. from Vathylakkos, and most other chalicotheriines.



**Fig. 2** General morphology of upper and lower molars and selected dental material of *Anisodon* sp. from Dorn-Dürkheim 1. **a** Diagrammatic view of a chalicotheriine upper molar. **Ac** anterior cingulum, **Av** anterior valley, **Cv** central valley, **El** ectoloph, **Hy** hypocone, **Lc** lingual cingulum, **Mss** mesostyle, **Mt** metacone, **Mtl** metaloph, **Mts** metastyle, **Pa** paracone, **Pac** paraconule, **Pas** parastyle, **Pf** postfossette, **Pr** protocone.

**b** Diagrammatic view of a chalicotheriine lower molar. **Bc** buccal cingulum, **End** entoconid, **Hyd** hypoconid, **Hyld** hypolophid, **Mtcd** metacristid, **Mtd** metaconid, **Mtsd** 'metastylid', **Pad** paraconid, **Pald** paralophid, **Pc** posterior cingulum, **Prd** protoconid, **Prld** protolophid, **Tal** talonid basin, **Trig** trigonid basin.

**c** Left M3 (DD 240) in occlusal view. **d** Right M2 (DD 230) in occlusal view. **e** Right M1 (DD 499) in occlusal view. **f** Right P4 (DD 450) in occlusal view. **g** Left P3 (DD249) in occlusal view. **h** Left P2 (DD 242) in occlusal view. **i** Left DP4 (DD 255) in occlusal view. **j** Right DP3 (DD 4120) in occlusal view. **k** Right m3 (DD 466) in occlusal view. **l** Right m1 (DD 4699) in occlusal view. **m** Right p3 and p4 (DD 455) in occlusal view. **n** Same in lingual view. **o** Left p2 (DD 277) in lingual view. **p** Same in buccal view. **q** Right i (DD 151) in lingual view. **r** Same in labial view. **s** Right dp4 (DD 460) in occlusal view. **t** Left dp3 (DD 260) in occlusal view. **u** Right dp2 (DD 463) in lingual view. **v** Same in buccal view.



The lingual cingulum on the upper molars of *Anisodon* sp. from Dorn-Dürkheim 1 is moderately strong. The lingual cingulum is strong around the protocone in *C. goldfussi* from the Dinotheriensande, *Anisodon* sp. from Vathylakkos, and *B. rusingensis*. The lingual cingulum is weak or absent on the upper molars of *A. grande*, the Akkaşdağı chalicother, and *C. goldfussi* from Höweneegg.

The metacone on the upper molars is placed more lingually than or as lingually as the paracone. In this character (for M2: character 12; Anquetin et al. 2007, character 44), *Anisodon* sp. from Dorn-Dürkheim 1 resembles *A. macedonicus*, *Kalimantsia*, *C. goldfussi*, *A. sivalense*, and *B. rusingensis*.

The external wall of the metacone and metastyle (character 13) is straight and subperpendicular to the anteroposterior direction. The same state is seen in *C. goldfussi*. Anquetin et al. 2007, character 45) also saw this state in *A. macedonicus*, but the wall seems to be even straighter in *Anisodon* sp. from Dorn-Dürkheim 1. In *H. sinense* and *A. sivalense*, the wall connecting the metacone and metastyle is literally folded concavely.

The postfossette is wide on all upper molars, including M3, as in the Nikolsburg chalicother, *A. macedonicus*, *A. sivalense*, and *C. brevirostris*, but unlike in *C. goldfussi*.

As in the Akkaşdağı chalicother, *A. macedonicus*, and *Anisodon* sp. from Vathylakkos, the mesostyle of M2 does

not project buccally in *Anisodon* sp. from Dorn-Dürkheim 1. The mesostyle of the M2 does project buccally in most other comparative species.

In *Anisodon* sp. from Dorn-Dürkheim 1, M1 and M3 are wider than long. This relation is similarly found in *C. goldfussi*, and *A. macedonicus*. The size of the M1 of *Anisodon* sp. (for measurements, see Online Resource 1) is within the lower range of first upper molars of *C. goldfussi*, within the upper range of those of *A. grande*, smaller than those of the Akkaşdağı chalicotheres, and larger than the M1 of *Kalimantsia* and *A. macedonicus*.

The paraconule is present and completely isolated from the protocone on the upper molars (characters 8 and 10; Anquetin et al. 2007, characters 40 and 42). The enamel connection between the paraconule and the paracone is very low. This state resembles that seen in the chalicotheres from Akkaşdağı, *Anisodon* sp. from Vathylakkos, *B. rusingensis*, and *A. macedonicus*, although in the latter, the connection between paraconule and paracone is slightly higher.

#### Upper premolars

The morphology of P4 and P3 differs from that of the upper molars in that they are smaller, wider than long, and their ectoloph is straight. P2 is smaller and less molariform than P4 and P3, and roundish in outline in occlusal view.

On P4 of *Anisodon* sp. from Dorn-Dürkheim 1 (Fig. 2f), the hypocone is mostly invisible and completely fused with the protocone to form a single oval, elongated cusp. Sometimes, a separate eminence is visible on the posterior side of the protocone.

On the protoloph of P3 (Fig. 2g) and P4 of *Anisodon* sp., the paraconule is mostly connected to the paracone and often (but not always) isolated from the protocone (characters 6 and 7; Anquetin et al. 2007, characters 38 and 39). The development of the paraconule is relatively variable.

P3 and P4 of *Anisodon* sp. from Dorn-Dürkheim 1 (see Online Resource 1 for measurements) are approximately equal in size to those of *A. grande* and *A. macedonicus*, but smaller than those of *C. goldfussi* and from Akkaşdağı, and larger than those of *B. rusingensis*.

Cingula on P4 seem to be variable in *Anisodon* sp. from Dorn-Dürkheim 1. Generally, cingula on P3 and P4 are weaker in *A. grande* than in *C. goldfussi*.

Development of the parastyle on P3 is variable in the Dorn-Dürkheim 1 material, and the parastyle may appear as a very prominent cusp. It does not seem to be very prominent in *A. grande* and *C. goldfussi*. The P3 parastyle proves to be variable in *C. brevirostris* where it is larger on the right side than on the left of the holotype animal.

On P3, the hypocone and protocone are connected or even fused in *Anisodon* sp. from Dorn-Dürkheim 1, the same state as in *A. sivalense*, *H. sinense*, and probably *A.*

*macedonicus*. This character is uncertain for *C. brevirostris*, *C. goldfussi*, and *B. rusingensis*, whereas in *A. grande* and the chalicotheres from Akkaşdağı and Vathylakkos the hypocone and protocone are two distinct cusps.

The P2 of *Anisodon* sp. from Dorn-Dürkheim 1 (Fig. 2h) is wider than long (see Online Resource 1 for measurements). This is also the case in *A. macedonicus*, *A. sivalense*, *H. sinense*, and *A. grande* from Neudorf. In *C. brevirostris*, *C. goldfussi* from La Grive, and *B. rusingensis*, P2 is longer than wide (character 5; Anquetin et al. 2007, character 37)

#### Upper deciduous teeth

The DP4 of *Anisodon* sp. strongly resembles M1 in morphology, but is significantly smaller (Fig. 2i; Online Resource 1).

DP3 is also molariform. It can be distinguished from DP4 by its smaller size and relatively wider dimensions (Fig. 2j; Online Resource 1).

Both DP4 and DP3 of *Anisodon* sp. from Dorn-Dürkheim 1 are very similar to those of other anisodont chalicotheriines, e.g. *Anisodon grande* (cf. Zapfe 1979), and are lacking diagnostic characters.

#### Lower molars

The lower molars consist of two U-shaped or V-shaped halves, the trigonid and talonid, which open toward the lingual side of the tooth. A diagrammatic representation of the morphology of the lower molars is given in Fig. 2b. It is important to note that the cuspid labelled Mtsd and traditionally called the ‘metastyliid’ is actually, according to Hooker (1994), a twinned metaconid and thus not strictly homologous to the metastyliid of non-perissodactyls. Lower m2 and m3 resemble each other in size, and it is often hard to differentiate them. The m1 is much smaller than m2 and m3 (Fig. 2k cf. Fig. 2l).

The ‘metastyliid’ on the lower molars is weak or absent (character 18; Anquetin et al. 2007, character 51). This is also the case in *A. grande*, and *C. goldfussi* (not coded by Anquetin et al. 2007), *A. macedonicus*, and the m2 of *Anisodon* sp. from Vathylakkos. A stronger ‘metastyliid’ is visible on the lower molars of ?*C. styriacum*, the presumed *C. goldfussi* from Gaiselberg, and *Anisodon wuduensis* (Xue and Coombs 1985).

The buccal cingulum on the lower molars and premolars of *Anisodon* sp. from Dorn-Dürkheim 1 is weak to moderately strong and thereby stronger than in *A. grande*, *C. brevirostris*, and weaker than in *C. goldfussi*, *Anisodon* sp. from Vathylakkos, and ?*C. styriacum*. The reliability of this character is not certain.

The lower molars of *Anisodon* sp. from Dorn-Dürkheim 1 (see Online Resource 1 for measurements) resemble those of *A. macedonicus* in size.

### Lower premolars

The lower premolars of *Anisodon* sp. from Dorn-Dürkheim 1 are shown in Fig. 2m–p. As in other Chalicotheriinae, p3 and p4 are submolariform but smaller than the lower molars. The trigonid is higher than the talonid.

The lower p2 is elongated with a central protoconid flanked by a smaller cusp both anteriorly and posteriorly.

As in most other chalicotheriines, the entoconid on p4 is prominent. Only *?C. styriacum* has a weak entoconid. This character was incorrectly scored as weak for *A. grande* by Anquetin et al. (2007).

Premolar size (see Online Resource 1 for measurements) resembles that of *A. grande* and *A. macedonicus*.

### Lower incisors and canine

Lower incisors and canines of chalicotheriines are monocuspid and peg-like to spatulate in crown shape. Canines are usually larger than incisors.

Chalicotheriine lower incisors are present in Dorn-Dürkheim 1 in at least two different morphologies, but it cannot be determined for certain whether there were two or three lower incisors in the jaw of *Anisodon* sp. because all incisors found are isolated. Two or three lower incisors are also found in *A. grande* (Neudorf; Anquetin et al. 2007 did not score this character for *A. grande*), *A. macedonicus*, *C. goldfussi* from La Grive, *C. brevirostris*, and *B. rusingensis*. One or no incisors are found in *A. sivalense*, *H. sinense*, *Anisodon* sp. from Titov Veles, and *A. wuduensis*.

A lower canine was possibly present in the lower jaw of *Anisodon* sp. from Dorn-Dürkheim 1. One monocuspid isolated tooth in the Dorn-Dürkheim 1 material (DD 4182) is larger than the incisors and might represent a chalicotheriine canine. However, this tooth crown is not very distinctive morphologically. A broken lower jaw symphysis (DD 3320, see below) features an alveolus for p2 and a diastema anterior to that, but does not preserve a canine or the respective alveolus. Based on this poor evidence, we decided to code this character (character 4; Anquetin et al. 2007, character 36) as missing (?). The only chalicotheriine known to have lost the lower canines is *Hesperotherium sinense* (Qiu, 2002).

### Lower deciduous teeth

The morphology and the proportions of dp4 of *Anisodon* sp. resemble those of m1, but the dimensions are smaller (Fig. 2s; Online Resource 1). The ‘metastylid’ and metaconid are distinct cusps.

The dp3 is also molariform, but smaller than dp4 (Fig. 2t; Online Resource 1). The trigonid is comparatively narrow, so that the outline of the whole tooth in occlusal view tapers toward the anterior direction as in other chalicotheres.

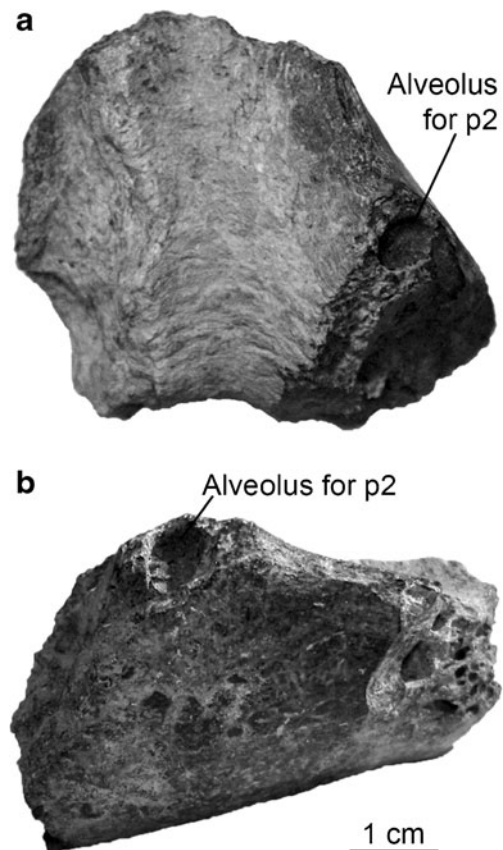
The dp 2 is a double-rooted tooth with an elongated crown in which a central protoconid is flanked by a smaller cusp both anteriorly (likely the paraconid) and posteriorly (likely the metaconid), and thus resembles the larger p2 in morphology.

As is the case with the upper deciduous teeth, no truly diagnostic characters could be defined for the lower deciduous teeth.

### Lower jaw symphysis

Among the remains of *Anisodon* sp. from Dorn-Dürkheim 1 is an anterior portion of the lower jaws including the robust, tightly fused symphysis (DD 3320). The left side of this specimen is heavily damaged, but the right side preserves the alveolus of p2 and a diastema anterior to it. The anteriormost end of this specimen is missing, and no incisors, canines, or their alveoli are preserved (Fig. 3a, b). The symphysis extends much farther back than the alveolus of p2 (Fig. 3a), and character 1 (posterior extent of the symphysis; character 33 of Anquetin et al. 2007) is coded as “level of the boundary of p3–p4” (1).

Whether or not there was a tuberosity on the ventral side of the lower jaw symphysis of *Anisodon* sp. from Dorn-



**Fig. 3** Lower jaw symphysis of *Anisodon* sp. from Dorn-Dürkheim 1 (DD 3320). **a** Dorsal (occlusal) view. **b** Right lateral view



Dürkheim 1 cannot be said with confidence, because the relevant part of the specimen is damaged. Thus, we coded this character (character 2; Anquetin et al. 2007, character 34) as missing (?).

### Carpals

The only preserved carpal in the chalicothere material from Dorn-Dürkheim 1 is a damaged left pisiform (DD 893). This stubby bone has a smaller articular facet for the ulna and a larger one for the cuneiform. Its sturdy shape is characteristic for the Chalicotheriinae and differs from the pisiformia of other perissodactyls, including schizotheriines. On the pisiform of *Anisodon* sp., the ulnar facet is broken off. This pisiform generally resembles that described for *A. grande* by Zapfe (1979) in shape and height, but appears to be wider mediolaterally (Online Resource 1).

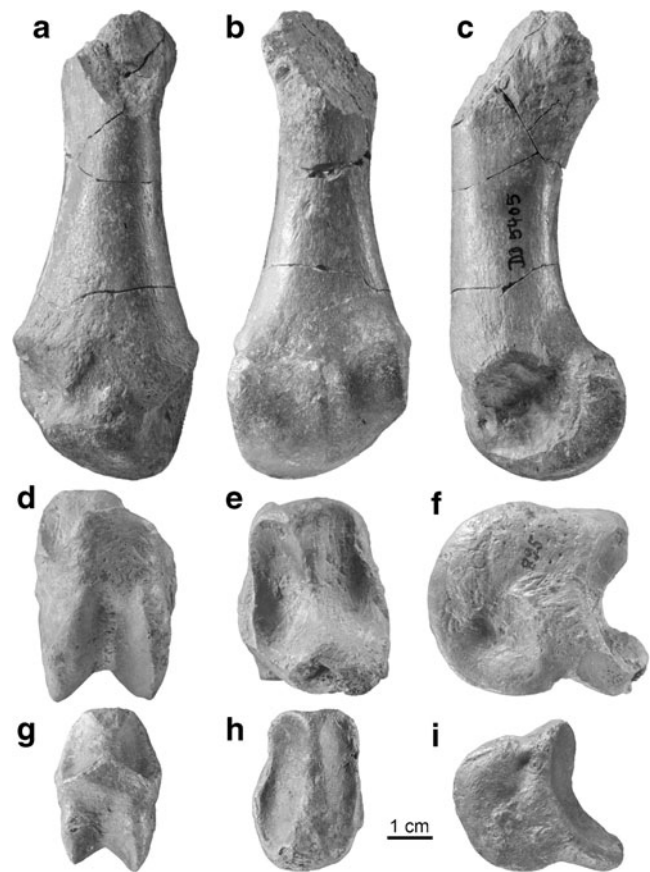
### Metacarpals

Chalicotheriinae have metacarpals II, III, and IV. These metacarpals are characterised by a broadened proximal and a roundish distal end, where they articulate with the carpals and other metacarpals, and proximal phalanges and sesamoids, respectively. The shaft is usually quite slender, which is why the metacarpals are prone to breakage and mostly only the joints are preserved.

The chalicothere material from Dorn-Dürkheim 1 contains a left Mc II with only the proximal end missing, the proximal end of a right Mc III, and one more distal metapodial epiphysis of unknown position.

The Mc II of *Anisodon* sp. from Dorn-Dürkheim 1 (DD 5405; Fig. 4a–c) comprises the shaft and the distal joint. The shaft widens distally, forming protuberances on the medial and lateral edges of the dorsal side of the bone, proximal to the distal joint. The dorsal side of the shaft is straight, while the palmar side is concave. The round articular surface for the proximal phalanx wraps around the distal end of the Mc II from dorsal to palmar, and is inclined to the medial side of the bone. Two parallel grooves on the palmar side articulate with the sesamoids. The morphology of this Mc II thus generally resembles that of *A. grande* described by Zapfe (1979). Although the full length of this specimen cannot be determined, it appears to be slightly sturdier than comparative material seen in the collections. The width of the Mc II of *Anisodon* sp. from Dorn-Dürkheim 1 (Online Resource 1), however, is less than that of *A. grande*, implying that its overall size was smaller.

The proximal end of the Mc III of *Anisodon* sp. from Dorn-Dürkheim 1 (DD 5406) shows the characteristic undercut on its lateral side that encloses the dorsopalmar elongated facet for the articulation with Mc IV. The proximal surface is divided into three subparallel articular facets:



**Fig. 4** Postcranial remains of *Anisodon* sp. from Dorn-Dürkheim 1. Left Mc II (DD 5405) in dorsal view (a), palmar view (b) and lateral view (c). Middle phalanx II of the left manus (DD 895) in dorsal view (d), proximal view (e) and lateral view (f). Middle phalanx of the right pes (DD 253) in dorsal view (g), plantar view (h) and medial view (i)

one slightly inclined toward the lateral side that articulates with the unciform, one steeply inclined toward the medial side that articulates with Mc II, and one directly proximal for articulation with the magnum. The dimensions of this Mc III (Online Resource 1) are smaller than those of the Mc III of *A. grande* (Zapfe, 1979) but larger than those of the Mc III of *Butleria rusingensis* (Butler 1965).

### Tarsals

The only preserved tarsals in the chalicothere material from Dorn-Dürkheim 1 are the medial (tibial) half of a left astragalus, and a left ectocuneiform.

The astragalus of *Anisodon* sp. from Dorn-Dürkheim 1 (DD 252) comprises the tibial condyle of the proximal articular surface for the tibia and the flat distal facet for the navicular. On the plantar side of the bone, the flat sustentacular facet for the calcaneum is visible, elevated above the level of the more concave medialmost extension of the ectal facet for the calcaneum. The distal surface bears a large, slightly curved facet for the navicular. The distal

surface is broken off on its lateral side so that it cannot be determined whether or not ectocuneiform and cuboid facets were present. The height of the condyle above the navicular facet (Online Resource 1) is relatively low in the astragalus from Dorn-Dürkheim 1 compared with that of *A. grande* (Zapfe 1979), and thus also relatively lower than that of *Chalicotherium goldfussi* (Schaefer and Zapfe, 1971).

The left ectocuneiform in the material of *Anisodon* sp. from Dorn-Dürkheim 1 is a relatively small, proximodistally flat bone with a roughly triangular outline in proximal view. The anteromedial edge of the bone is broken off. The flat proximal surface bears the facet for the navicular. This facet ends in a sharp ridge on its fibular side. There is no articular surface for the astragalus. This character seems to be variable in *Anisodon*, since an astragalus facet was noted by Zapfe (1979) for only two out of four ectocuneiform specimens of *A. grande* from Neudorf. The slightly concave distal surface of the ectocuneiform articulates with Mt III. There are steep, band-shaped articular surfaces for Mt II and the cuboid, respectively, on the medial and lateral sides of the bone. The ectocuneiform of *Anisodon* sp. from Dorn-Dürkheim 1 seems to be slightly smaller than that of *A. grande* from Neudorf, with a narrower mediolateral width at a comparable proximodistal height of the bone (Online Resource 1; cf. Zapfe 1979).

### Phalanges

Chalicotheriid middle phalanges are generally proximodistally shortened and do not have a corpus or shaft. The proximal articular surface has two subparallel grooves for articulation with the distal condyles of the proximal phalanx. The distal trochlea is high in the dorsovolar direction and mediolaterally compressed, having a semicircular outline in lateral view.

Two middle phalanges of *Anisodon* sp. are preserved in the material from Dorn-Dürkheim 1: one middle phalanx of the manus, most likely of the second digit of the left side (Fig. 4d–f), and one middle phalanx of an undetermined digit of the right pes (Fig. 4g–i). The middle phalanx of the manus is relatively large with a mediolaterally broad palmar flange of the proximal joint (Online Resource 1). Its dimensions are in good accordance with the ones of middle phalanx II of the hand of *A. grande* from Neudorf (Zapfe 1979) and middle phalanges of the hand of *A. salinus* (AMNH 19436). Assignment to the second digit is corroborated by the asymmetrical shape of the proximal joint. Middle phalanges in the comparative material of the manus of *C. goldfussi* (BSPG 1959 XIII 15) and *C. brevirostris* (AMNH 26536) are generally overall longer and higher, and even more compressed mediolaterally. Those of *Butleria rusingensis* are overall smaller (Butler 1965).

The middle phalanx of the pes of *Anisodon* sp. from Dorn-Dürkheim 1 is overall smaller than the one of the hand (Online

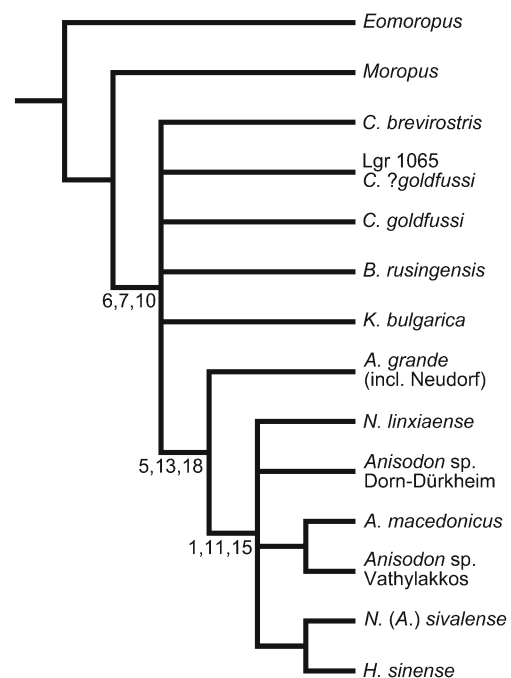
Resource 1). Its proximal joint is symmetrical except for a widening of the articular surface on the medial side, so that it is difficult to determine the digit of this phalanx. This phalanx of the pes fits relatively well in the size range of phalanges of the pes of *A. grande* (Zapfe, 1979), but it is less robust (i.e. less wide in relation to the other dimensions). Its dimension and robustness resemble that of middle phalanges of the pes of *A. salinus* (AMNH 19436). The middle phalanges of the pes of *C. brevirostris* (AMNH 26518 and 26536) are overall higher and narrower, while those of *Butleria rusingensis* are overall smaller (Butler 1965).

## Results

### Phylogeny

From the character matrix of 18 characters and 14 taxa, 20 most parsimonious trees with a length of 29 steps were produced (CI=0.59; RI=0.71). Their strict consensus tree with a length of 33 steps (CI=0.52; RI=0.62) is shown in Fig. 5.

Although monophyly of the Chalicotheriinae has traditionally been based on postcranial characters (Coombs 1989), it is also supported in both Anquetin et al. (2007) and our analysis by three dental synapomorphies: P3 protoloph stopping at the paraconule (character 6, RI=0.25), P4 protoloph stopping at the paraconule (character 7, RI=1), and protoloph on upper molars not reaching the protocone (character 10, RI=0.5).



**Fig. 5** Phylogenetic analysis of the Chalicotheriinae: strict consensus tree of 20 most parsimonious trees based on 18 characters and 14 taxa. Tree length is 33 steps; CI=0.52; RI=0.62

Within the Chalicotheriinae, the existence of an *Anisodon* clade that includes *A. grande*, *Anisodon* sp. from Dorn-Dürkheim 1, *N. linxiaense*, *Hesperotherium sinense*, *N. sivalense* (= *Anisodon sivalensis*), *Anisodon* sp. from Vathylakkos, and *A. macedonicus* is confirmed. Monophyly of the *Anisodon* clade is supported by three dental synapomorphies: P2 is wider than long (character 5, RI=1), the external wall of the metacone and metastyle on M3 is subparallel to anteroposterior lengthening (character 13, RI=0.75), and the ‘metastyloid’ of the lower molars is weak (character 18, RI=0.75).

Within the *Anisodon* clade, *Anisodon* sp. from Dorn-Dürkheim 1 falls within a clade that also includes *N. linxiaense*, *Hesperotherium sinense*, *N.* (= *A.*) *sivalense*, *Anisodon* sp. from Vathylakkos, and *A. macedonicus*, but excludes *A. grande*. This clade is supported by three synapomorphies: the lower jaw symphysis extends posteriorly to the level of p3–p4 (character 1, RI=0.6), the anterior cingulum displays a notch in front of the protocone (character 11, RI=0.5), and the posterior cingular crest on M3 reaches the hypocone summit (character 15, RI=1). Within this clade, *A. macedonicus* forms a clade with *Anisodon* sp. from Vathylakkos, and *H. sinense* forms a clade with *N.* (= *A.*) *sivalense*. The exact positions of *Anisodon* sp. from Dorn-Dürkheim 1 and *N. linxiaense* within this clade are unresolved.

The relationships between *Kalimantsia bulgarica*, *Butleria rusingensis*, *Chalicotherium goldfussi*, *C. ? goldfussi* from La Grive, and *Chalicotherium brevirostris* are not resolved in the strict consensus tree. Therefore, the existence of a monophyletic *Chalicotherium* clade that includes *C. goldfussi* and *C. brevirostris* cannot be supported using dental characters only (see “Discussion”).

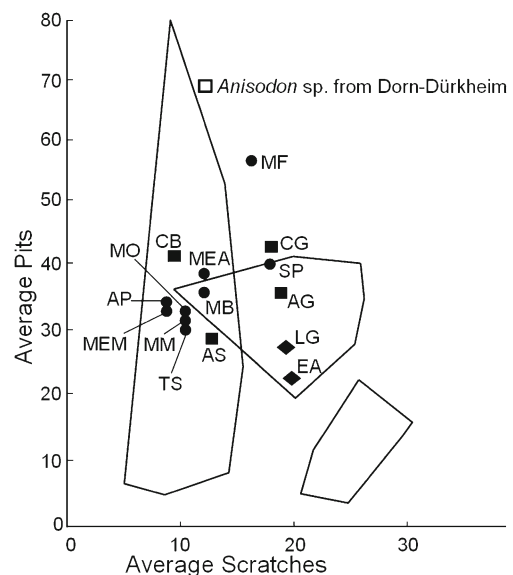
Closer examination of the individual most parsimonious trees provides some more information on what topologies are best supported. The *Anisodon* clade is supported in all 20 trees, as are the clades formed by *A. macedonicus* with *Anisodon* sp. from Vathylakkos and *H. sinense* with *N.* (= *A.*) *sivalense*. *A. grande* always turns out as the sister taxon of the rest of the *Anisodon* clade.

In 10 out of 20 cases, *Anisodon* sp. from Dorn-Dürkheim 1 is the sister taxon of a clade formed by *A. macedonicus*, *Anisodon* sp. from Vathylakkos, *H. sinense*, and *N.* (= *A.*) *sivalense*. Additionally, in 1 case, it is the sister taxon of the *A. macedonicus*-Vathylakkos clade only. In 9 out of 20 cases, *Anisodon* sp. from Dorn-Dürkheim 1 forms a clade with *N. linxiaense*.

The positions of the chalicotheres that are not members of the *Anisodon* clade vary from tree to tree. The only obvious pattern noted among these chalicotheriines is an affinity of *C. goldfussi* and *C. ?goldfussi* from La Grive that form a clade in 13 out of 20 most parsimonious trees.

## Microwear

Figure 6 shows the patterns of microwear seen in extant grazers, extant leaf-dominated browsers, and extant fruit-dominated browsers (after Solounias and Semprebon 2002; Semprebon et al. 2004) represented by convex hulls. Data for *Anisodon* sp. from Dorn-Dürkheim 1 analysed in this study is compared to those for other fossil chalicotheres that were studied by Semprebon et al. (2011). The average number of scratches versus the average number of pits (at  $\times 35$  magnification) per taxon is represented. The average number of scratches has more discriminatory power than the average number of pits for segregating extant leaf-dominated browsers versus grazers, as there is no overlap in average scratch numbers between these two trophic groups, although pit numbers may overlap between them. Teeth of extant fruit-dominated browsers show relatively more pitted enamel than those of grazers and many leaf-dominated browsers, and most individuals have large pits relatively deeply inscribed in their enamel. While there is no overlap between extant grazing and leaf-dominated browsing taxa in the average number of scratches found, fruit-



**Fig. 6** Microwear analysis: binary plot of the number of total pits versus the number of total scratches of *Anisodon* sp. from Dorn-Dürkheim 1 (open square) compared with other Chalicotheriidae (filled symbols). Basal chalicotheres (diamonds): EA *Eomoropus amarorum*, LG *Litolophus gobiensis*, Chalicotheriines (squares): AG *Anisodon grande* (BSPG), AGN *Anisodon grande* (Neudorf), AS *Anisodon salinum*, CB *Chalicotherium brevirostris*, CG *Chalicotherium goldfussi*, Schizotheriines (circles): AP *Ancylotherium pentelicum*, MB *Metaschizotherium bavaricum*, MF *Metaschizotherium fraasi*, MEA *Moropus elatus* (Agate Quarry), MEM *Moropus elatus* (Morava Ranch), MM *Moropus merriami*, MO *Moropus oregonensis*, SP *Schizotherium priscum*, TS *Tylocephalonyx skinneri*. Convex hulls are drawn around modern ungulate leaf browsers (left), fruit browsers (centre), and grazers (right). Comparative data from Semprebon et al. (2011)

dominated browsers show a wider spectrum of scratch results and often fall in the gap between browsers and grazers.

It is clear from Fig. 6 that *Anisodon* sp. from Dorn-Dürkheim 1 does not have average scratch/pit results typical of extant grazers but falls closer to the extant browsing morphospaces, although it has more pits than most extant browsing forms studied thus far and more pits than other fossil chalicotheres that have been studied. When additional microwear variables are considered (Table 2), it is apparent that the enamel is not gouged in most individuals but that all individuals have both large and small pits. In addition, scratches in most individuals vary between coarse and hypercoarse in terms of their textures. Some individuals display puncture-like pits typical of fruit consumption.

## Discussion

### Morphological comparison and phylogenetic placement of *Anisodon* sp. from Dorn-Dürkheim 1

The absence hitherto of chalicotheres of the *Anisodon* clade in Central Europe from MN 7 onwards previously led to the preliminary conclusion that the Dorn-Dürkheim 1 chalicothere, being MN 11 in age, must belong to *Chalicotherium goldfussi*, which was around at least as late as MN 9 (Franzen 1981). However, morphological characters, such as a P2 that is wider than long (character 5, RI=1), unequivocally place the Dorn-Dürkheim 1 chalicothere within the *Anisodon* clade rather than with *Chalicotherium*. Further, *Anisodon* sp. from Dorn-Dürkheim 1 allies with representatives of the *Anisodon* clade from the MN 11–13 of southeastern Europe and Asia rather than with *A. grande* from the MN 6 of Germany (Fig. 5). This finding suggests that the Dorn-Dürkheim 1 chalicothere is not a direct descendant of Central European Chalicotheriinae but arrived in Central Europe during the MN 10–11 faunal turnover, as part of an immigration wave, possibly from the southeast, that also brought other large mammals, e.g. ruminants from the Greco–Iranian region, to Dorn-Dürkheim 1 (Franzen in Franzen and Storch 1999; Vislobokova 2005).

Unfortunately, the Dorn-Dürkheim 1 material is rather fragmentary. On the one hand, no single distinctive morphological character was found that is unique to this chalicotheriine and would therefore justify the erection of a new species. On the other hand, there are morphological differences from most of the comparative material (rather minor ones within the *Anisodon* clade), so that clear assignment to any of the existing species is also not possible.

In the following, we review the Chalicotheriinae, including remarks regarding morphological differences between these species or specimens and *Anisodon* sp. from Dorn-Dürkheim 1.

The type material of *Chalicotherium goldfussi* Kaup, (1833) comes from the Dinotheriensande of Eppelsheim (MN 9), Germany. Kaup (1833) also named a very similar but much smaller Eppelsheim species, *Chalicotherium antiquum*, later generally synonymised with *C. goldfussi* (see, e.g. Butler 1965). Eppelsheim material of *C. goldfussi* includes numerous teeth but little skull and postcranial material. For this reason, it has been difficult to do any complete comparison of *C. goldfussi* with other Chalicotheriinae. Nonetheless, most MN 9 and later chalicotheriine material collected in Europe was until recently automatically placed in or near *C. goldfussi*. The work of de Bonis et al. (1995), Geraads et al. (2001), and Anquetin et al. (2007) has gradually revealed a greater diversity of European late Miocene Chalicotheriinae.

To complicate things further, Böhme et al. (2012) and Pickford and Pourabrishami (2013, this issue) have suggested that the classical Dinotheriensande localities, including Eppelsheim, contain reworked deposits that span a much longer time than only the MN 9. Sediments of the Eppelsheim Formation contain faunal elements that indicate ages reaching back into the early Miocene (MN 4/5) and on into the late Miocene (MN 11) or possibly even the early Pliocene. If this is true, it must be considered that the chalicotheriid remains from the Dinotheriensande could represent more species than only *C. goldfussi*, with the later ones being contemporary and possibly conspecific with the Dorn-Dürkheim 1 chalicothere. Currently, however, this scenario is mere speculation, and would require more detailed comparison of dental material from various Dinotheriensande localities (Eppelsheim, Esselborn, Wissberg, Westhofen, etc.). Our preliminary examination suggests that most or all of the Dinotheriensande chalicothere material falls within the range of dental variation that might be expected for *C. goldfussi*.

*Anisodon* sp. from Dorn-Dürkheim 1 is altogether smaller and differs from *C. goldfussi* from the Dinotheriensande in many morphological aspects: the cingula on its upper and lower molars are weaker, the central valley and the gap between the protocone and the hypocone are narrower, the protocone projects less far lingually, the mesostyle projects less far buccally, and the protoloph is shorter (stops at the paraconule). The postfossette on M3 is wider in *Anisodon* sp., and the posterior cingular crest reaches further up the hypocone. Furthermore, the height of the medial condyle of the astragalus is lower, and the middle phalanges of the manus are shorter in the proximodistal direction and lower in the dorsopalmar direction.

Anquetin et al. (2007) also referred material from Höwenegg (Germany, MN 9) to *C. goldfussi*. The upper molar from Höwenegg, however, differs from those in the Dinotheriensande material by appearing to be more angular in outline in occlusal view and by having a weaker lingual cingulum. It also differs from *Anisodon* sp. from Dorn-Dürkheim 1 in these characters.



Heissig (2009) described a small amount of chalicothere material, including an isolated p4 from Atzelsdorf (Austria), identifying it as *Chalicotherium goldfussi*. He cited the age of the Atzelsdorf fauna as basal MN 9, corresponding to the Vienna Basin Pannonian Zone C. Although the Atzelsdorf p4 resembles specimens of *Anisodon* sp. from Dorn-Dürkheim 1 generally in having a well-developed entoconid, it is clearly larger (26.1 mm in length; Heissig 2009), consistent with its referral to *C. goldfussi*.

Zapfe (1949a) included *Chalicotherium goldfussi* in the fauna from Gaiselberg near Zistersdorf (Austria) but did not figure any of the material. An m2 from Gaiselberg shows a well-developed ‘metastyloid’, which is not the case in lower molars of *Anisodon* sp. from Dorn-Dürkheim 1. The Mt III from Gaiselberg was subsequently figured elsewhere (Schaefer and Zapfe 1971; Zapfe 1949b, 1979), but there is no Dorn-Dürkheim 1 Mt III to compare with it.

Additional important material of *C. goldfussi*, including a maxilla and mandible with teeth and a jaw symphysis with alveoli, has been described and figured by de Bonis et al. (1995) and Anquetin et al. (2007) from Saint-Gaudens (France, MN 8). The jaw symphysis is particularly important in demonstrating the presence of three small lower incisors in addition to the canine in *C. goldfussi*. As for *Anisodon* sp. from Dorn-Dürkheim 1, it is not possible to establish the exact number of lower incisors (two or three), since only isolated incisors are preserved.

Anquetin et al. (2007) gave particular attention to cranial and dental material from La Grive St.-Alban (France, MN 7–8) originally described by Depéret (1892) as a race of *Macrotherium grande*, *M. grande rhodanicum*, transitional between *M. grande* and *C. goldfussi*. De Bonis et al. (1995) allied this material with *C. goldfussi* as *C. goldfussi* race *rhodanicum*. Both their analysis and that of Anquetin et al. (2007) placed the La Grive chalicotheriine skull close to or within *C. goldfussi* and well removed from *Anisodon grande*. This skull shows how dramatically the cranial proportions of *Chalicotherium* and *Anisodon* differ.

*Anisodon* sp. from Dorn-Dürkheim 1 differs from *Chalicotherium goldfussi* from La Grive by having a wider P2 and a shorter protocone on P3. The anterior cingulum bears a notch in front of the protocone on the upper molars, the postfossette on M3 is wider, and the posterior cingular crest reaches farther up the hypocone. *Anisodon* sp. also has a weaker ‘metastyloid’ on its lower molars and the lower jaw symphysis appears to extend farther posteriorly.

Abel (1922) figured a palate and proximal phalanx from Nikolsburg (= Mikulov, Czech Republic; MN 9). This palate has generally been referred to *C. goldfussi*, though it differs in some ways from *C. goldfussi* from the Dinotheriensande and probably should be reevaluated. The metacone in upper molars of *Anisodon* sp. from Dorn-Dürkheim 1 lies more

lingually and the mesostyle projects less far buccally than in the Nikolsburg chalicothere.

Bach (1912) named *Chalicotherium styriacum* for a left lower jaw with four cheek teeth in place and additional anterior alveoli. The jaw comes from the Lehmbachmühle near Eggersdorf in southeastern Steiermark, Austria, from beds attributed by Mottl (1970) to the lower Pannonian (earliest onset of the Vallesian according to de Bonis et al. 1995: MN 9). Bach identified the teeth as p3, m1, m2, and m3, but they are likely p4–m3, as noted by Mottl (1966). De Bonis et al. (1995) examined a cast of the type mandible in the British Museum and included it in their analysis, attributing it to *Macrotherium grande*, but Anquetin et al. (2007) did not use it, citing questions about the identity of the cheek teeth. Personal observation (M.C.C.) has confirmed identification of the lower teeth as p4–m3. There are also alveoli preserved anterior to p4: apparently two (but filled in by matrix) for the roots of p3 and one for p2. The p2 is not raised above the level of the diastema, and the lower jaw symphysis extends only as far as the posterior end of the p2 alveolus. The diastema anterior to the p2 alveolus is quite short (~16.8 mm), and there is another alveolus, for the canine, at its anterior end. The canine alveolus preserves some of the tooth root in its deeper part, and its anterior end forms a notch in the jaw margin. No signs of incisor alveoli are preserved. We refer to this material as ?*Chalicotherium styriacum*, though its exact affinities and the validity of the species remain unevaluated. *Anisodon* sp. from Dorn-Dürkheim 1 has a weaker ‘metastyloid’ and a weaker buccal cingulum on the lower molars, and a larger entoconid on p3 and p4 than ?*C. styriacum*. There is thus no reason to refer the Dorn-Dürkheim 1 material to this species.

Pethö (1885) named a new chalicothere species, *Chalicotherium baltavarensis*, from Baltavar (Hungary, MN 13). It is based on a small lower jaw, preserved in Budapest, which was neither figured nor measured. Pethö observed a canine alveolus. No specimen number for the holotype is available in the literature, but Butler (1965), studying a cast (BMNH M10597), tentatively identified the small but molariform lower tooth in the jaw as a small dp4 and suggested that the specimen was a juvenile representative of *C. goldfussi*. It is likely that Butler’s taxonomic assignment was based primarily on the geologic age being much later than *Anisodon grande*, since *A. macedonicus*, a European late Miocene anisodont, had not yet been identified. We have not been able to compare this material with *Anisodon* sp. from Dorn-Dürkheim 1 but mention it primarily for completeness, since it needs to be reevaluated to improve our understanding of Turolian Chalicotheriinae in Eastern Europe.

*Chalicotherium brevirostris* (Colbert, 1934) is primarily based on a skull and some postcranial material from the Tunggur Formation, middle Miocene (equivalent to MN 7–8), Inner Mongolia, China. Despite its name, *C. brevirostris*

does not have a particularly short muzzle compared to anisodont Chalicotheriinae. It was placed in the genus *Chalicotherium* by Anquetin et al. (2007), though de Bonis et al. (1995) found more ambiguous relationships. Very recently, Liu and Zhang (2012) described and figured two mandibles collected in the 1980s from the Tunggur Formation and referable to *C. brevirostris*. The two Tunggur mandibles and associated teeth are clearly different from lower jaws and teeth from Hebei Province and the Qinghai-Tibetan Plateau referred to *Chalicotherium* cf. *brevirostris* by Hu (1959) and Wang and Wang (2001). Liu and Zhang (2012) regarded the differences as sufficient to exclude the jaws previously referred to *C. cf. brevirostris* from this species. Therefore, we have included only the newly described Tunggur lower jaws along with the type skull in our comparison of *C. brevirostris*.

The morphology of *Anisodon* sp. from Dorn-Dürkheim 1 differs significantly from that of *C. brevirostris*. *Anisodon* sp. has a wider P2, the protoloph on its upper molars does not reach the protocone, the protocone lies more lingually, and the mesostyle projects less far buccally than in *C. brevirostris*. Additionally, the anterior cingulum on the upper molars of *Anisodon* sp. from Dorn-Dürkheim 1 has a notch in front of the protocone, the postfossette on M3 is wider, and the posterior cingular crest on M3 reaches up the hypocone. Lower molars of *Anisodon* sp. have a weaker ‘metastylid’ than those of *C. brevirostris*. There is some similarity between *Anisodon* sp. from Dorn-Dürkheim 1 and *C. brevirostris* in the development of the lower jaw symphysis. The jaw symphysis ends posteriorly opposite p3, and *C. brevirostris* clearly has three lower incisor alveoli, increasing in size from i1 to i3, as well as a well-developed canine alveolus (Liu and Zhang 2012). Unfortunately incomplete preservation of the symphysis in *Anisodon* sp. from Dorn-Dürkheim 1 and the lack of in-place preservation of anterior teeth prevent a more thorough comparison. Postcranially, *Anisodon* sp. from Dorn-Dürkheim 1 differs from *C. brevirostris* in having middle phalanges of the manus that are shorter in the proximodistal direction and lower in the dorsopalmar direction, and middle phalanges of the pes that are mediolaterally wider and lower in the dorsoplantar direction.

Geraads et al. (2001) named a new chalicothere genus and species, *Kalimantsia bulgarica*, from the locality Kalimantsi-Pehtsata (MN 11–12) in southwestern Bulgaria. The holotype and only clearly referable specimen is a skull, which is crushed transversely and does not preserve a number of features that would aid in its interpretation. The skull is quite long posterior to the orbit, but the snout is relatively short. P3–M3 are preserved in place. Anquetin et al. (2007) were unable to study the type skull but scored it on the basis of the original description for 15 characters, which when analysed placed *Kalimantsia* in a relatively basal position among the Chalicotheriinae. Although the age of Kalimantsi-Pehtsata is

somewhat comparable to Dorn-Dürkheim 1, it is unlikely that the Dorn-Dürkheim 1 chalicothere is referable to *Kalimantsia*. In *K. bulgarica*, the upper molars (especially M3) are more elongated than those of typical Chalicotheriinae, but this is not true of upper molars from Dorn-Dürkheim 1. The upper molars of *Anisodon* sp. from Dorn-Dürkheim 1 are less angular in occlusal view, the protocone is positioned less lingually and the mesostyle less buccally, the anterior cingulum of the upper molars has a notch anterior to the protocone, and the M1 of *Anisodon* sp. is larger.

Clearly, there is much to be learned about Turolian chalicotheres from Bulgaria, because the schizotheriine chalicothere *Ancylotherium* is also present at Kalimantsi-Pehtsata as well as at the somewhat later Bulgarian site Hadjidimovo 1 (Geraads et al. 2001). Hadjidimovo 1 also preserves a complete left manus of a chalicotheriine referred to *Chalicotherium* ? sp., cf. *Chalicotherium goldfussi* by Geraads et al. (2001). The exact taxonomic placement of this manus remains uncertain and awaits broader comparison of postcranial elements among mid-to-late Miocene Chalicotheriinae. It is not yet clear what part the limited chalicothere postcranial material from Dorn-Dürkheim 1 can play in such a comparison.

The genus *Anisodon* is based on *Anisodon grande* (de Blainville, 1849), which at various times has been called *Macrotherium grande* (for example, de Bonis et al. 1995) or *Chalicotherium grande* (for example, Butler 1965; Zapfe 1979). Geraads et al. (2001) made a good case for the priority of the name *Anisodon*. The type and additional material of *A. grande*, which comes from Sansan (France, MN 6), have recently been redescribed in detail and discussed by Anquetin et al. (2007). Zapfe (1979) made a monographic study of material from cave fissure fills at Neudorf (Slovakia, MN 6), referring his large collection of adult and juvenile dental and postcranial material to this species, now *A. grande*. Anquetin et al. (2007) did not include the Neudorf material in their analysis because they had concerns whether all the material was indeed *A. grande*. However, both J.M.F. and M.C.C. have examined this material independently and see no reason to doubt reference of most or all of it to *A. grande*. We therefore include the Neudorf material in our comparisons of *A. grande*, as did Semprebon et al. (2011) in their analysis of dental microwear.

Although its teeth are generally the same size, *Anisodon* sp. from Dorn-Dürkheim 1 differs from *A. grande* in that it has stronger cingula on the upper and lower molars, with the lingual cingulum on M1 bearing a notch in front of the protocone, and the posterior cingular crest on M3 reaching further up the hypocone. The central valley and the gap between the protocone and the hypocone are wider on the Dorn-Dürkheim 1 upper molars than in *A. grande*, and the metacone lies more lingually. The external wall of the metacone and the metastyle is at a larger angle with the anteroposterior direction

in the upper molars. On P3, the hypocone is less distinct. The lower jaw symphysis extends farther posteriorly. Furthermore, the postcranial material of *Anisodon* sp. from Dorn-Dürkheim 1 is mostly smaller, and the middle phalanges of the pes are less robust. The height of the medial condyle of the astragalus is lower than in *A. grande*.

A number of mid-to-late Miocene localities in Spain have yielded fragmentary specimens referable to Chalicotheriinae (Villalta and Crusafont 1945; Cerdeño and Alberdi 2006). Generally the mid-Miocene (Aragonian) specimens have been referred to what is now *Anisodon grande*, whereas Vallesian (MN 9 and MN 10) materials are cited as *Chalicotherium goldfussi* (Cerdeño and Alberdi 2006). Some Turolian specimens (MN 11 or MN 12) have been allied with *Anisodon*. Chalicotheres from the Iberian Peninsula are important in the light of the suggestion that some other elements of the Dorn-Dürkheim 1 fauna, e.g. cervids, have affinities to taxa from southwestern Europe (Azanza et al. 2013, this issue). Unfortunately, we were not able to study the Spanish specimens and little of the most relevant material has been figured, but we recommend additional study and the inclusion of this material in future phylogenetic studies on chalicotheriine chalicotheres.

*Anisodon salinus* (Forster Cooper, 1922) is based on fragmentary material covering a substantial temporal range in the middle to late Miocene of the Siwalik Group in Pakistan. It is possible that more than one species may be represented. Anquetin et al. (2007) did not review this taxon, but Semperebon et al. (2011) suggested that all or most of the material belongs to an anisodont comparable to *A. grande*. Chen et al. (2012) also referred this species to *Anisodon*. *Anisodon* sp. from Dorn-Dürkheim 1 resembles *A. salinus* in many aspects that reflect their common referral to the anisodont clade, including the wide postfossette, posterior cingular crest reaching the hypocone summit, and weak ‘metastylid’. Both have a distinct paraconule that is isolated from the protocone. On the other hand, there are differences in some details of the teeth. For example, the external wall of the metacone and metastyle on upper molars is very straight and subperpendicular to the antero-posterior axis of the tooth in *Anisodon* sp. from Dorn-Dürkheim 1. The lower jaw of *A. salinus* figured by Pickford (1982) has a symphysis extending to the anterior end of p3, which is not as far posterior as that of the Dorn-Dürkheim 1 chalicother.

*Anisodon macedonicus* was erected as a new species of *Macrotherium* by de Bonis et al. (1995). The holotype includes a well-preserved skull, lower jaws, atlas, and axis from Dytiko 3 (MN 13), Macedonia, Greece. Anquetin et al. (2007) referred the species to *Anisodon*. The completeness of the skull and dentition of the holotype places *A. macedonicus* in a strong comparative position for identifying late Miocene European anisodont material. Symeonidis (1973) described and figured a palate with left and right P3–M3, identifying it

as *Chalicotherium goldfussi*. The specimen comes from Chomateri near Pikermi (Greece; MN 12–13). It was reassigned by de Bonis et al. (1995) to *Macrotherium macedonicum* (now *Anisodon macedonicus*).

*Anisodon* sp. from Dorn-Dürkheim 1, however, most likely does not belong to *A. macedonicus*, since, on its upper molars, the protocone lies more posterior and less lingual, and its metacone is positioned more lingually. The M1 is altogether larger than that of *A. macedonicus*, and the external wall of the metacone and metastyle is subperpendicular rather than subparallel to the anteroposterior direction.

Arambourg and Piveteau (1929) described a partial skull, left mandible, and isolated teeth and postcranials from Salonica (Greece), referring it to *Chalicotherium* cf. *goldfussi*. The locality, Vathylakkos, is generally dated as MN 11. The Vathylakkos material was referred by de Bonis et al. (1995) to *Macrotherium macedonicum*. Anquetin et al. (2007) coded it as “Vathylakkos” in their analysis, where it was placed among the derived anisodonts and was reassigned as *Anisodon* sp.

*Anisodon* sp. from Dorn-Dürkheim 1 differs from *Anisodon* sp. from Vathylakkos in only a very few aspects: the protocone on its upper molars is positioned more posteriorly, the metacone on its M2 more lingually, and the hypocone on its P3 is less distinct. Furthermore, *Anisodon* sp. from Dorn-Dürkheim 1 has weaker cingula on its upper and lower molars.

Saraç and Sen (2005) described and figured a juvenile skull with left P3–M3 and right M1–M3 (M3 partly erupted on both sides) from Akkaşdağı (Turkey). They identified the skull as *Ancylotherium pentelicum* (Schizotheriinae), whose postcranial remains also occur in the fauna, but, based on relatively low crown height and the morphology of the squared (not elongated) teeth, it clearly belongs to a member of the anisodont clade of the Chalicotheriinae. The age of the Akkaşdağı fauna is given as Turolian. The teeth on this specimen are little worn, and so provide a great opportunity for comparison. It is possible that this specimen represents a juvenile individual of *A. macedonicus*, but more detailed analysis is necessary.

The Dorn-Dürkheim 1 chalicother differs from the Akkaşdağı specimen by having slightly smaller upper molars and premolars, a stronger cingulum on the upper molars, and a less distinct hypocone on P3.

The referral to *Chalicotherium goldfussi* by Schaefer and Zapfe (1971) of a robust mandible from Henndorf (Austria, MN 12–13) has caused much subsequent confusion in understanding the lower jaw morphology of *Anisodon* versus *Chalicotherium*. Partly because of this mandible, the possibility of a radiation of late Miocene anisodonts was long ignored. Lower jaws that were also placed in *Chalicotherium* on the basis of resemblance to the Henndorf mandible include the type of “*Chalicotherium*” *wuduensis* Xue and Coombs (1985) from China and material from Titov Veles (Macedonia, MN



12) described by Garevski and Zapfe (1983). Anquetin et al. (2007) reassigned all these mandibles to *Anisodon*. Both *Anisodon* sp. from Titov Veles and *A. wuduensis* have completely lost their lower incisors, whereas *Anisodon* sp. from Dorn-Dürkheim 1 has at least two lower incisors. The ‘metastylid’ of *A. wuduensis* is more strongly developed than that of *Anisodon* sp. from Dorn-Dürkheim 1; the stronger ‘metastylid’ also distinguishes *A. wuduensis* from most other anisodont species.

Chen et al. (2012) recently named *Nestoritherium linxiaense*, a new species of late Miocene anisodont Chalicotheriinae from China. The species is well represented by a skull with teeth and additional referred cranial, dental, and mandibular material. In describing *N. linxiaense*, Chen et al. (2012) analysed a revised data matrix based on that of Anquetin et al. (2007) but included additional Asian taxa. Their results suggested two monophyletic anisodont clades, *Anisodon* and *Nestoritherium*, with *N. linxiaense* as the basal species of *Nestoritherium*. Other members of Chen et al.’s *Nestoritherium* clade are the type species *N. sivalense* (*A. sivalensis* of Anquetin et al. 2007), *N. wuduense* (*A. wuduensis* of Anquetin et al. 2007), and *Hesperotherium sinense*. *N. linxiaense* resembles other members of the *Nestoritherium* clade and differs from *Anisodon* sp. from Dorn-Dürkheim 1 in having weak or absent lower incisors and a weak paraconule on upper molars. Compared to other species of *Nestoritherium* and to *Anisodon macedonicus*, the mandibular symphysis of *N. linxiaense* is relatively short (character 37 of Chen et al. 2012).

The latest survivors of the anisodont clade of Chalicotheriinae are found in the Pleistocene of Asia. These include *Nestoritherium sivalense* (Falconer and Cautley, 1843) from the Siwaliks. *Anisodon* sp. from Dorn-Dürkheim 1 does not belong to this species, because, in contrast to *N. sivalense*, it has lower incisors. Other morphological differences include the presence of a paraconule on the upper molars, a notch in the anterior cingulum in front of the protocone and an altogether less angular shape of the upper molars. Additionally, the external wall of the metacone and metastyle on M3 is subperpendicular to the anterior direction, and the mesostyle on M2 projects less far buccally in *Anisodon* sp. from Dorn-Dürkheim 1.

Limited material from the Chinese Pleistocene was originally named *Chalicotherium sinense* by Owen (1870) but later placed in *Nestoritherium* by Colbert and Hooijer (1953). More recently, Qiu (2002) named a new genus *Hesperotherium* on the basis of better material, and additional specimens have since been reported. *Hesperotherium sinense* lacks all canines and incisors, and its lower jaw symphysis extends posteriorly to p4 but is much reduced anteriorly. The premolars are extremely short. *Anisodon* sp. from Dorn-Dürkheim 1 differs from *H. sinense* by having lower incisors (and possibly a canine), a larger

paraconule on the upper molars, and a less buccally projecting mesostyle on M2.

*Chalicotherium rusingense* from the early Miocene of East Africa was described by Butler (1965) based on dental, cranial and postcranial material. De Bonis et al. (1995) assigned the species to the genus *Butleria*. *B. rusingensis* is commonly viewed as a basal sister taxon of later chalicotheriines from Eurasia (Anquetin et al. 2007), though our more limited analysis did not resolve this position.

*Anisodon* sp. from Dorn-Dürkheim 1 is larger in body size and has a relatively wider P2 than *B. rusingense*. The lingual cingulum on its upper molars and the ‘metastylid’ of its lower molars are weaker. Additionally, the symphysis of the lower jaw extends further back in *Anisodon* sp. Because of its relatively basal nature, much earlier temporal range, and distant geographical occurrence, *B. rusingensis* is not a candidate for taxonomic assignment of the Dorn-Dürkheim 1 material and is only included here for completeness.

#### Discussion of phylogenetic results

The results of our phylogenetic study show that the Dorn-Dürkheim 1 chalicothere is a member of the *Anisodon* clade (Fig. 5). Furthermore, in the majority of the most parsimonious trees, it is associated with members of the genus *Anisodon*. Therefore, the assignment of the Dorn-Dürkheim 1 material to *Anisodon* sp. based on the description and comparison with other chalicotheriines is corroborated by the phylogenetic analysis.

Previous phylogenetic studies like that by Anquetin et al. (2007) have stressed the importance of the use of cranial characters in addition to dental characters because of a generally relatively high variability of dental characters in chalicotheres. The chalicotheriine material preserved in Dorn-Dürkheim 1, however, does not include cranial elements beyond the partial mandibular symphysis and therefore does not permit the use of cranial characters.

Despite this limitation of our study, and despite the exclusion of *Anisodon wuduensis* and *Anisodon* sp. from Titov Veles from the matrix and the use of all unordered characters, our results are still consistent with the general chalicotheriine relationships discovered in the more comprehensive phylogenies by Anquetin et al. (2007) and, to a lesser extent, by de Bonis et al. (1995).

In Anquetin et al. (2007) and de Bonis et al. (1995), *Butleria* is the sister taxon of all post-early Miocene Chalicotheriinae. This relationship could not be resolved in our study, based on dental characters only. In our analysis, there is no monophyletic *Chalicotherium* clade, in contrast to results in Anquetin et al. (2007) when *Kalimantsia* was excluded. However, when they included *Kalimantsia*, as we did, the apparent monophyly disappeared (Anquetin et al. 2007, fig. 10 cf. fig. 11).



*Nestoritherium sivalense* is clearly associated with the *Anisodon* clade in our phylogeny, thus corroborating the results of Anquetin et al. (2007) and contradicting de Bonis et al. (1995), who found “*Nestoritherium*” to be related to *Chalicotherium* rather than *Anisodon*. The existence of a *Nestoritherium* clade containing *N. (=A.) sivalense*, *N. linxiaense*, *H. sinense*, and *A. wuduensis* as a sister taxon of the *Anisodon* clade as suggested by Chen et al. (2012) cannot be confirmed here, and Fig. 5 shows *N. sivalense*, *N. linxiaense*, and *H. sinense* scattered within the *Anisodon* clade. While *N. sivalense*, and *H. sinense* form a clade, the exact position of *N. linxiaense* is not determined. These results call for additional future revision of chalicotheriine taxonomy and potential adoption of the suggestion by Anquetin et al. (2007) to synonymise *Nestoritherium* with *Anisodon*, and use the genus name *Anisodon* for all members of the *Anisodon* clade. However, a more comprehensive phylogenetic study is beyond the scope of this paper, for which a smaller analysis was sufficient to support the assignment of the Dorn-Dürkheim 1 material to *Anisodon* sp.

Based on our own observations on the comparative material, recent literature (e.g. Liu and Zhang 2012), and the inclusion of additional material (e.g. the Neudorf material in *Anisodon grande*), we re-coded several of the characters used by Anquetin et al. (2007) as follows:

We coded lower incisors (character 3) as absent (0) or present (1), thereby following de Bonis et al. (1995, character 37), but reversing the coding in order to make it consistent with the coding used for the absence or presence of canines (character 4). Anquetin et al. (2007) coded lower incisors (character 35) as absent (0), two (1), or three (2). We would not have been able to apply this scheme for the Dorn-Dürkheim 1 material, because we know that at least two different morphologies of incisors are present, but it is not certain whether there are two or three lower incisors.

The paraconule of the upper molars of the holotype of *C. brevirostris* is unusual for a chalicotheriine chalicothere in having rather strong connections with both the paracone and the protocone (character 10; contrary to the coding by Anquetin et al. 2007, character 42).

Character state “1” of character 10 (protoloph on upper molars; character 42 of Anquetin et al. 2007) was renamed “not reaching the protocone or absent” in order to keep the binary coding of Anquetin et al. (2007) but also to accommodate for *Nestoritherium* and *Hesperotherium* that do not have a protoloph (Chen et al. 2012, character 47).

The anterior cingulum on the upper molars (character 11; Anquetin et al. 2007, character 43) displays a notch in front of the protocone in all of the examined comparative material of *C. goldfussi*, and was therefore re-coded as (1). The entoconid of p4 is prominent in *A. grande*, even if the Neudorf material (prominent entoconid on p4) is not included. Other material, e.g. from the MN 6 of Thannhausen

(BSPG 1974 I25), also shows a prominent entoconid on p4 (character 17; Anquetin et al. 2007, character 49). The development of the ‘metastyloid’ on the lower molars (character 18) was not scored for *C. goldfussi* by Anquetin et al. (2007, character 51). We are including material from the Dinotheriensande (e.g. SMNK PA 3823-25) that clearly shows that the ‘metastyloid’ is weak and therefore re-coded this character as (0) for *C. goldfussi*.

In terms of character use in future phylogenetic analysis, we made the following observations. The trigonid of the lower molars was scored by Anquetin et al. (2007, character 50) as either U-shaped or V-shaped. Revisiting scored specimens of various species, we found that this character is very variable, and that it may not be applicable to all lower molars equally (m1 seems to be generally more V-shaped than m2 and m3). The curvature of the lophs of the trigonid might additionally be altered by wear. Because of these issues, we decided to omit this character and do not recommend its use in future studies. Furthermore, contra Anquetin et al. (2007, character 50), it should be the protolophid (not the hypolophid) that does or does not reach the metaconid.

The development of the ‘metastyloid’ on the lower molars (character 18; Anquetin et al. 2007, character 51) can be rather variable as well. Anquetin et al. (2007) miscoded it as “weak” for *A. wuduensis* (not included in our analysis; cf. Xue and Coombs 1985). Additionally, the connection of the paraconule with the paracone and the protocone on the upper premolars (characters 6 and 7; Anquetin et al. 2007, characters 38 and 39) seem to vary quite a bit within species. We decided to leave characters 6, 7, and 18 in the analysis, but the degree of variation and the species that show variation of these characters should generally be re-examined. Such a reconsideration can then be the basis for deciding whether it is reasonable to continue to use these characters in phylogenetic analyses.

Characters of the lower dentition and mandible were coded for *C. brevirostris* according to the description by Liu and Zhang (2012). The entoconid of p4 (character 17) of *C. brevirostris* was coded “conspicuous” based on the figures provided by Liu and Zhang (2012), although the authors described the entoconid as low.

Furthermore, further research may make the inclusion of more characters (e.g. lingual projection of the protocone of the upper molars, connection of hypocone and protocone of P3) possible.

#### Palaeoecology of the Dorn-Dürkheim 1 chalicothere

Our results suggest that *Anisodon* sp. from Dorn-Dürkheim 1 were most likely browsers on the basis of enamel microwear scratch and pit values and that grass was not a likely part of their dietary regime. This conclusion is consistent with prior microwear studies that classified fossil chalicotheres as browsers (Coombs and Sempebon 2005;

Semprebon et al. 2011; Schulz et al. 2007). This conclusion is also supported by the characteristics of the dentition of chalicotheres which are similar to those of many browsing ungulates. Even so, the studies above have suggested that, while chalicotheres were apparently browsing, microwear and other tooth wear patterns (i.e., mesowear) are unusual in terms of typical browsing patterns.

Solounias and Semprebon (2002) have shown that extant browsers that browse on relatively soft materials (i.e. leaves), in addition to possessing relatively low scratch numbers, generally have predominantly finely textured scratches and relatively few if any large pits. Conversely, browsers that browse on relatively coarse materials (e.g. bark and fruit), typically possess many large pits and relatively few finely textured scratches. In addition, fruit browsing is discernible by symmetrical, deep and puncture-like large pits.

Our microwear results for *Anisodon* sp. from Dorn-Dürkheim 1 include many pits (both large and small), coarse and hypercoarse scratch textures, and medium- and small-sized puncture pits in some individuals. *Anisodon* sp. from Dorn-Dürkheim 1 thus most likely consumed a fairly abrasive browsing diet. Schulz et al. (2007) reached similar conclusions for *A. grande* on the basis of mesowear (gross cusp molar wear; see Fortelius and Solounias 2000).

Based on the results of our microwear analysis, relatively hard fruits, in addition to leaves and twigs, were probably also occasionally incorporated into the dietary regime. Both microwear (Semprebon et al. 2011) and mesowear (Semprebon et al. 2009) studies of other European chalicotheres suggest more fruit browsing than is postulated for North American chalicotheres, which overall display less abrasive mesowear signatures. Further, *Anisodon* sp. from Dorn-Dürkheim 1 may have occupied a more open environment than other studied European chalicotheres as evidenced by its higher pit counts, although the lack of heavy gouging of dental enamel suggests that grit was not likely a significant factor in dental wear.

Dental stereomicrowear results are consistent with the interpretation of the Dorn-Dürkheim 1 area as a tropical savannah or subtropical grassland to woodland during MN 11, based on the reconstruction of body masses and analysis of theoretical biomass (Costeur et al. 2013, this issue).

The presence among the *Anisodon* sp. material from Dorn-Dürkheim 1 of at least nine adult and four juvenile individuals furthermore suggests that no ecological or taphonomic segregation between juveniles and adults took place, and that the Dorn-Dürkheim 1 locality represents the environment where chalicotheres actually dwelt.

## Conclusions

Morphological and phylogenetic analyses of the Dorn-Dürkheim 1 chalicothere clearly show that it belongs among

other Chalicotheriinae of the *Anisodon* clade rather than with *Chalicotherium*.

Within the *Anisodon* clade, the closest morphological resemblance is noted with *A. macedonicus* from Greece and *Anisodon* sp. from Vathyakkos. Further morphological similarities are noted with material from the Miocene Siwaliks of southern Asia. However, diagnostic characters are too scarce for an assignment on the species level.

The closer resemblance of *Anisodon* sp. from Dorn-Dürkheim 1 to representatives of *Anisodon* from the MN 11–13 of Greece and Asia than to *A. grande* from the MN 6 of Central and Western Europe, suggests that our *Anisodon* sp. is not a direct descendant of Central European Chalicotheriinae but arrived during the MN 10–11 faunal turnover, as part of an immigration wave from southeastern Europe.

Microwear analysis revealed that the diet of *Anisodon* sp. from Dorn-Dürkheim 1 likely included leaves and hard fruit. These results are concordant with the interpretation of the Turolian Dorn-Dürkheim 1 environment as a woodland savannah.

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