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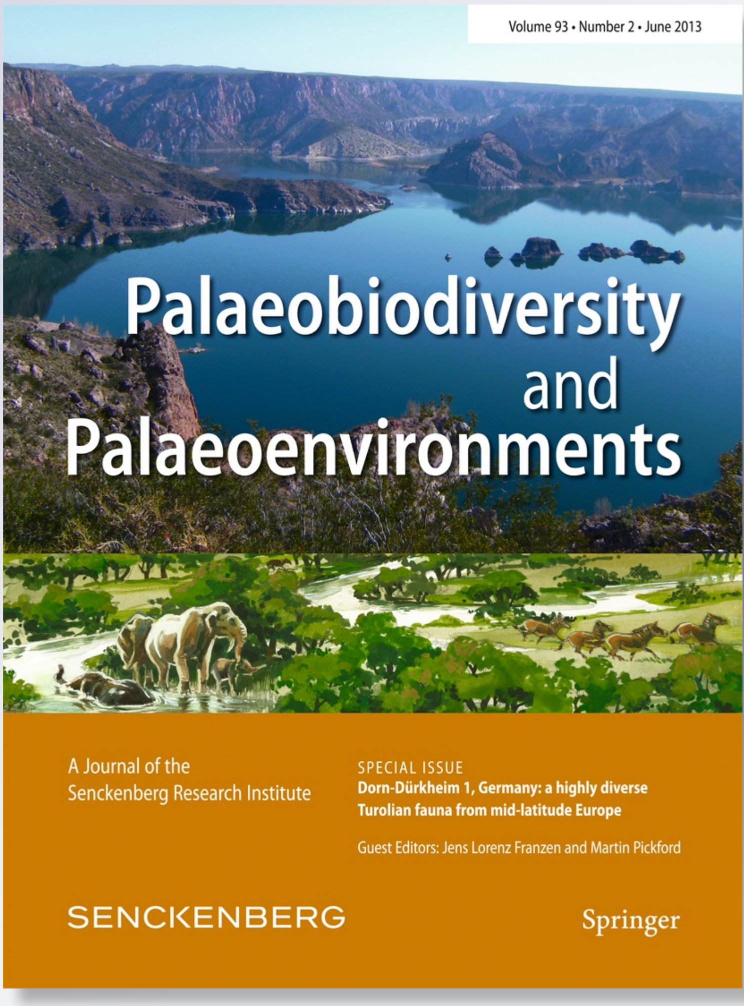

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ORIGINAL PAPER

The early Turolian (late Miocene) Cervidae (Artiodactyla, Mammalia) from the fossil site of Dorn-Dürkheim 1 (Germany) and implications on the origin of crown cervids

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Abstract Dental and cranial appendage remains of Cervidae from the fossil site of Dorn-Dürkheim are studied in detail. The material mainly includes isolated teeth, isolated pedicles and antler pieces. Neither tooth rows nor complete appendages are recorded. Comparative morphology and statistics of morphometrics (principal component analysis and discriminant analysis) allow for the classification of small and large dentitions, small cranial appendages, two morphotypes of large pedicles and two morphotypes of large antlers. Possible combinations of the classified units document the sympatric occurrence of three species, namely, *Procapreolus* sp., Muntiacinae gen. and sp. indet., cf. *Cervavitulus mimus*, but the fragmentary condition of the material leads to ambiguity regarding their composition and, consequently, to a certain extent regarding the taxonomic identification. However, these remains indicate the contemporaneous occurrence of early Turolian members of the crown cervids Muntiacinae and Capreolinae and close a previous spatiotemporal gap in the European cervid record. In addition, their presence proves the progressive turnover from dichotomous-antlered muntiacines to early monopodial-antlered crown cervids from NE to SW Europe in the late Miocene. The taxonomical assignment challenges the recent hypothesis on the origin of crown Cervidae around the middle/late Miocene border since Dorn-Dürkheim cervids provide further evidence for the successive achievement of derived characters in cranial appendages of crown cervids (mediopostorbital position and backwards orientation of pedicles, coronet development, shaft development/elongation, beam development and increase in number of antler tines) in the lineage of crown cervids, which originated during the middle Miocene.

Keywords Muntiacinae · Capreolinae · Comparative morphology · Morphometrics · Cranial appendages · Dentition

This article is a contribution to the special issue "Dorn-Dürkheim 1, Germany: A highly diverse Turolian fauna from mid-latitude Europe".

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Introduction

Members of the family Cervidae are defined as pecoran ruminants with the synapomorphy of paired frontal outgrowths which consist of a perennial proximal pedicle that carries the temporary, distal and more or less regularly cast branched antler (e.g. Janis and Scott 1987). Owing to their abundance as typical faunal components, fossil remains of Cervidae are recorded from the early Miocene onwards in Eurasia (e.g. Azanza 1993; Azanza 2000; Gentry et al. 1999; Obergfell 1957; Rössner 1995). The generally continuous fossil record gives a good idea of antler and dentition evolution (Azanza 1993; Gentry 1994; Gentry et al. 1999), although the latter has not been studied in detail for the entire evolutionary history of cervids. However, regional gaps in the Neogene geological record impede our knowledge of the evolutionary history of cervids and obscure the origin of crown cervids [living deer, their nearest common ancestor, and all of the extinct taxa derived from that common ancestor (subfamilies Cervinae, Capreolinae)] in the late middle Miocene (European Land Mammal Mega-Zone late Astaracian) and late Miocene (European Land Mammal Mega-Zones Vallesian and Turolian). In this context, the cervids from the fossil site of Dorn-Dürkheim (Rheinhessen, Germany) cover a crucial spatiotemporal unit.

Late Miocene Cervidae

Among early Miocene faunas *Procervulus* seems to show what an early relative of later deer might have been like. Its antlers can be shed, and they consist of two terminating points mounted on long fairly upright pedicles above the orbits. Such two-branched or dichotomous antlers continue to be found in the middle Miocene cervids. The antlers of these deer become larger and show increasingly clear signs of being deciduous, especially when coronets (also called burrs or roses) evolve that mark the severance points at the bases of the antlers (Fig. 1a). In the Vallesian (early late Miocene) faunas, cervids with dichotomous antlers, such as *Euprox* Stehlin, 1928, a survivor from the middle Miocene, and *Amphiprox* Kaup, 1839 were the predominant representatives of this group. Their taxonomic status as true Muntiacinae (or Muntiacini) has been proposed (Azanza 1993, 2000; Azanza and Montoya 1995) based on cranial appendages with true coronets and strongly inclined pedicles in side view—characters that clearly separate them from stem cervids, the early and middle Miocene dicrocerines [*Dicrocerus*, *Acteocemas*, *Stehlinoceros* (most probably junior synonym of *Paradicrocerus*)] and procervulines (*Procervulus*, *Heteroprox*). In Western Europe, these putative two-branched muntiacines were replaced during the Turolian (late late Miocene) by monopodial two- and three-tined cervids. The monopodial construction of antlers (Fig. 1b), i.e. a beam with offshoots of tines (Bubenik 1990), is a typical characteristic of crown cervids. Notwithstanding that the shaft of the *Amphiprox* antlers shows a clear trend towards the formation of a beam (i.e. the bifurcation mid-point is displaced from the shaft axis towards the periphery; see Fig. 1), the monopodial construction is first recorded in *Lucentia*, a putative holometacarpal Vallesian and early Turolian deer with two tines (Azanza and Montoya 1995; Gentry 2005). Three-tined monopodial antlers with the first tine set high above the coronet (a construction which is still preserved in extant *Capreolus*) are common in the middle to late Turolian cervids *Cervavitus* Khomenko, 1913, *Pliocervus* Hilzheimer, 1922, *Procapreolus* Schlosser, 1924, *Croizetoceros* Heintz, 1970, *Pavlodaria* Vislobokova, 1980, *Turiacemas* Azanza, 2000 and in other forms not yet formally

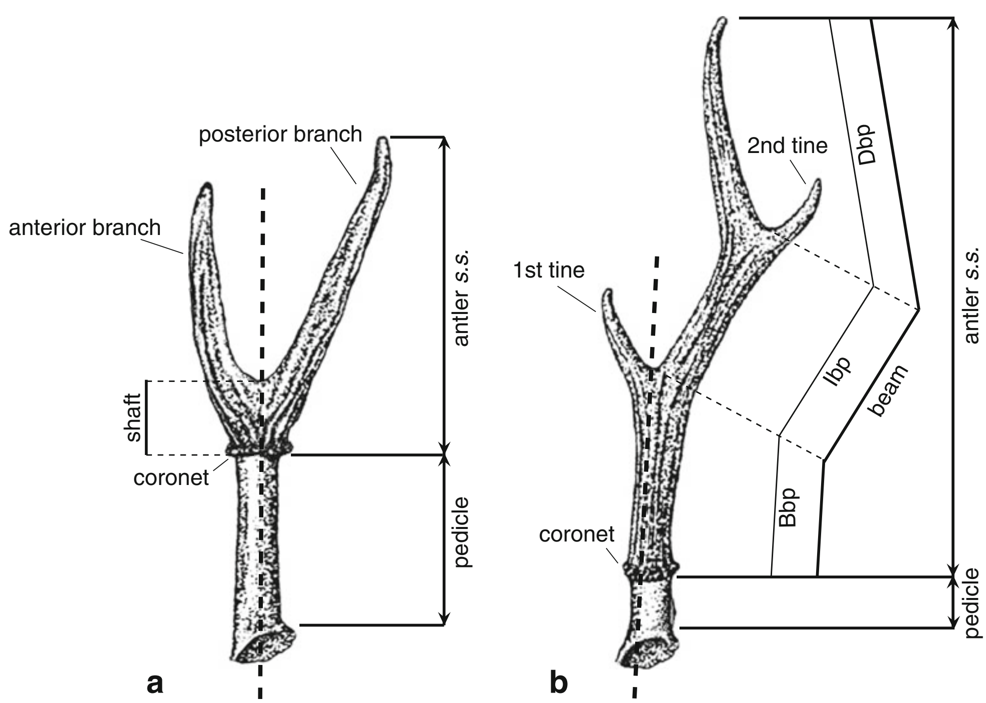


Fig. 1 Antler nomenclature (modified from Azanza 2000). **a** Dichotomous construction. If the angle bisector is traced on the bifurcation, the mid-point of the bifurcation is placed on the longitudinal shaft axis. **b** Monopodial construction. The mid-point of the bifurcation is displaced towards the periphery of the beam. *Bbp* Basal beam portion; *lbp* intermediate beam portion; *Dbp* distal beam portion

established. These Turolian cervids do not represent a distinct clade within the Cervidae because *Cervavitus*, *Procapreolus* and *Pavlodaria* are considered to be the earliest known representatives of Cervini, Capreolini and Rangiferini, respectively (Czyzewska 1968; Korotkevich 1963; Petronio et al. 2007; Vislobokova 1980; among others). Rather, they are an assemblage of genera possessing a suite of primitive characters such as moderately long pedicles, holometacarpal state, moderately elongate upper canines and variously developed external postprotocristid (*Palaeomeryx* fold) and external postprotocrista (protoconal fold in Heintz 1970). Accordingly, the transition between Vallesian and Turolian faunas of cervids must have occurred in Western Europe during the early Turolian. However, available fossils in most of the early Turolian localities are so scarce or fragmentary that a definite determination is not possible (see appendix, Table 1). In Eastern Europe, however, three-tined monopodial cervids seem to have occurred earlier in the Vallesian (Böhme et al. 2012; Vislobokova 2007). In addition, a dichotomous antler construction with a moderate to long shaft (Fig. 1a) is evident for the contemporaneous putative muntiacines *Euprox*, *Amphiprox* and the later *Paracervulus* Teilhard and Trassaert, 1937. Taken together, scarce or fragmentary material is difficult to classify, with the common high degree of antler variability presenting an additional challenge as this can easily lead to an incorrect taxonomic determination and subsequent biostratigraphic misinterpretation (see Böhme et al. 2012). Moreover, the antlers of *Amphiprox anocerus*, the only species of the genus, are typified by a shaft showing a clear trend toward the formation of a beam. Thus, late Miocene two-tined muntiacines (*Euprox*, *Amphiprox*, *Paracervulus*) and representatives of three-tined cervid clades (such as *Cervavitus* or *Procapreolus*) can be easily misclassified. In fact, *Cervavitus bessarabiensis* Lungu, 1967 from the early Vallesian faunas of Kalfa and Buzhor in Moldova (Lungu 1984) and *Cervavitus sarmaticus* Korotkevich, 1970 described in the Late Vallesian of Krivoi Rog in the Ukraine (Korotkevich 1970, 1988), have been more recently ascribed to *Euprox* (Vislobokova 2007).

The best known early Turolian cervid is *Lucentia* Azanza and Montoya, 1995 in Western Europe and *Cervavitus variabilis* Alexeev, 1915 in Eastern Europe. *Lucentia* is the first cervid with clear monopodial antlers, but two-tined as nothing indicates a second offshoot of the beam. Azanza and Montoya (1995) signalled that three-tined specimens should have been found if *Lucentia* had borne them because the richest material (from Crevillente 2, Spain) comprises mainly adults according to dental remains. The morphological pattern of *Lucentia* antlers is similar to that of the three-tined Turolian cervids which have a beam carrying the first off-shot at a very high level above the coronet. This makes the *Lucentia* antler a good candidate for the transitional state from dichotomous long-shafted antlers towards three-tined monopodial ones. This genus is a common taxon in the early Turolian, and no older localities in Spain, but it could have been present during the early Vallesian in Eastern Europe, as some material from Rudabanya (European Land Mammal Zone MN9, Hungary) has been ascribed to it (Gentry 2005). In turn, *Cervavitus variabilis* is described from Novoelisavetovka (MN11, Ukraine) with palmated three-tined antlers that are more complex than those of other *Cervavitus* species (Petronio et al. 2007). Alexeev (1915) noted that it was plesiometacarpalian, but subsequent authors have ignored her assertion, and the holometacarpalian condition of the later Chinese *C. shanxius* (material from Henan and Shanxi provinces, late late Miocene; Dong 2011) means that it is probably safe to do so. All other medium-sized species reliably assigned to the early Turolian are imperfectly known, and only preliminary data have been published to date. Notwithstanding that their antlers show no indication of third tines or second bifurcations, they were ascribed to *Cervavitus, Turiacemas* and *Procapreolus* (see appendix, Table 1).

Putative muntiacines seem to be also present in the early Turolian (see appendix, Table 1). Azanza (2000) reported very scarce material of a Muntiacinae gen. and sp. indet. from the fossil site Crevillente 2 (Spain). However, only pedicles and teeth are known. A relatively small number of remains from Csákvár (Hungary; Kretzoi 1951) and Kohfidisch (Austria; Vislobokova 2007) are reported to belong to *Euprox*, but no antlers have been illustrated, and Vislobokova (2007) signalled that poor preservation does not permit species determination. According to a photograph (kindly provided by L. Kordos) of specimen V.11368 from Csákvár (Kretzoi 1951), the adscription to at least muntiacines seems to be justifiable.

A very small species, whose affinities are uncertain, has also been recorded in Csákvár and preliminarily described as *Cervavitulus mimus* by Kretzoi (1951). Some dental and postcranial elements from early Turolian fossil sites of Piera (Spain) and Aubignas I (France) have been assigned to it (Azanza et al. 1993).

The cervids found in the German locality of Dorn-Dürkheim 1 can be assigned to these already known early Turolian forms. In taxonomic lists, Franzen and Storch (1975) and Franzen (1981) signalled the presence of the small *Cervavitulus mimus* and further reported a medium-sized deer assigned to the three-tined *Turiacemas concudensis* that was common in Spanish and French middle Turolian (MN 12) localities (Azanza 2000; Azanza et al. 1993). Moreover, Franzen and Storch (1975) listed the presence of the muntiacine *Amphiprox anocerus*, but Franzen (1981) eliminated this from the taxonomic list at a later date. The aim of our paper is to provide an in-depth investigation and description of the morphology and size of the Dorn-Dürkheim 1 cervid remains, their systematic assignment, and a discussion of their contribution to the question of early late Miocene cervid phylogenetics.

Biochronology and faunal context of Dorn-Dürkheim 1

The vertebrate locality Dorn-Dürkheim 1 is situated about 25 km south of the city of Mainz (Germany). The fossiliferous levels consist of up to almost 2 m of fluviatile gravel, sand, and claystone and are heavily affected by Pleistocene cryoturbation. The sediments are interpreted as deposits of an oxbow or tributary of the early Rhine River characterised by frequently changing hydrodynamics (Franzen 1997a; Franzen 2013, this issue; Franzen and Schäfer 1981; Franzen et al. 2013, this issue).

Dorn-Dürkheim 1 is correlated with the Turolian subordinate European Mammal Neogene Zones MN11 (Mein 1975) and is the hitherto only German locality securely correlated with the Turolian. It has provided one of the most species-rich (more than 80 mammal species) and northernmost Turolian faunas in Europe (Franzen 1997b). Thus, it constitutes a decisive biogeographic tie-point between Turolian faunas from the southwestern and eastern realms (Gentry and Kaiser 2009).

A preliminary faunal list was published by Franzen and Storch (1975, 1999) and Franzen (1981). In-depth studies on micromammals (Franzen and Storch 1975; Storch 1978; Storch and Dahlmann 2000) and part of the macromammal fauna (carnivores by Morlo 1997 and Roth and Morlo 1997; mastodonts by Gaziry 1997; hipparions by Bernor and Franzen 1997 and Kaiser et al. 2003; rhinoceroses by Cerdeño 1997; pigs by Made Van der 1997; bovids by Gentry and Kaiser 2009) have been published to date. As a whole, the fauna indicates a forested biotope with an abundantly watered landscape (Franzen and Storch 1999; but see Costeur et al. 2013, this issue).

Material and methods

Since 1973, the site of Dorn-Dürkheim 1 has been the object of several field seasons, and a rich collection of fossils is stored at the Senckenberg Forschungsinstitut (Frankfurt am Main, Germany). By far the greater part of the ruminant remains in the Dorn-Dürkheim 1 collection belongs to Cervidae. However, these remains are represented by only very fragmentary antler remains, predominantly isolated teeth, missing fragmentary tooth rows with more than three teeth, and some postcranial elements. Hence, the reconstruction of antler morphology and the association of corresponding teeth and bones is a very difficult task, as is the assignment of the material to the two or three species in previous taxonomic lists.

Nomenclature

The nomenclature used in the anatomical description of cranial appendages (Fig. 1) follows Azanza et al. (1989) and Azanza (2000). For the teeth we used Bärmann and Rössner (2011).

Measurements

Distances used for antler and tooth measurements are defined in Azanza (2000).

Abbreviations

DD = Dorn-Dürkheim 1. Three-tined monopodial antlers consist of a beam with offshoots of two tines; thus the beam is divided in three parts: Bbp = Basal beam portion (= b-span in Petronio et al. 2007); Ibp = intermediate beam portion; Dbp = distal beam portion. Measurements: L, length; H, height of the shaft measured on the medial side at the mid-point of the bifurcation; PAD, proximal anteroposterior depth; PTW, proximal transversal width; DAD, distal anteroposterior depth; DTW, distal transversal width; Wa, tooth width measured on the anterior lobe; Wp, tooth width measured on the posterior lobe.

Statistical analyses

The morphometrical analysis of cranial appendages was greatly limited by the high degree of bone fragmentation in DD deposits. Only the appendage specimens with preserved complete pedicle or complete Bbp are included. Pedicles and antlers s.s. have been analysed separately because only one specimen comprises the complete Bbp attached to the pedicle. A total of eight linear measurements (see appendix, Table 2) were used to reflect the size and shape of the pedicle and antler shaft/Bpb. For comparative purposes, several fossil cervid species of different European sites were included. All of these have antlers with a moderate (1.5 < H/PTW <3.0) or long (H/PTW >3.0) shaft/Bbp. Among the muntiacines we included some Vallesian forms: *Amphiprox anocerus* from Eppelsheim (Germany; MN 9), *Amphiprox* cf. *anocerus* from Can Llobateres (Spain; MN 9) and “*Euprox*” aff. *minimus* from Terrassa (Spain; MN 10) (B.A., unpublished data). We also included metric data of “*Paracervulus*” *australis* from Montpellier (France; MN 14; Azanza 2000), which seems to be the latest muntiacine in southwestern Europe. For Cervinae and Capreolinae, we included species referred to the two-tined genus *Lucentia*, to the three-tined genera *Turiacemas*, *Pliocervus* and *Procapreolus* and to the three-tined species

Croizetoceros pyrenaicus (Azanza 1995, 2000). We also included data on the extant *Capreolus* stored at the Senckenberg Forschungsinstitut (Frankfurt am Main, Germany) because its antlers have kept the Turolian three-tined construction (BA, unpublished data).

The computational work was done using the NTSYS-PC statistical programs ver. 1.80 (Rohlf 1993) and the Statagraphics program v. 5 (STSC Inc, Knoxville, TN). Data were analysed by two methods: principal component analysis (PCA), and discriminant analysis (DA). PCA was used to seek out the occurrence of heterogeneities in the data set. To reduce the basic data matrices, we compiled the data of each cervid species using the sample mean and its lower and upper confidence limits for each measurement on the antlers. Character-by-character correlation was obtained from each matrix by calculating the Pearson product-moment correlation coefficient between each pair of character in each set. These matrices served as input in the PCA. The PCA was performed on each character-by-character correlation matrix, and three factors were extracted. The character factor loadings were used to calculate the operational unit factor scores, or projections, in the two-factor spaces.

DA was used to account for correlated variables and to identify those characters most useful in discriminating members of different groups, as well as to assess the probability that specimens without precise taxonomic determination could be correctly assigned to different a priori groups. Using DA, we maximised differences between a priori designate groups relative to within-group variability. Thus, a number of canonical discriminant functions were derived (with the maximum number of functions equal to the number of predefined groups minus one) as linear functions of the original variables weighted by coefficients (equal to the number of variables), computed so that group means on the function were as different as possible and computed also under the condition that values on successive functions were not correlated with values on preceding functions. A discriminant score was calculated for each specimen, from each of the derived functions using the observed character values for that individual. These scores represent that specimen's coordinates in the canonical variates space. DA was thus used as an ordination procedure to display the group pattern in unidimensional, bidimensional or three-dimensional plots that emphasise the differences existing between the predesigned groups. To assign DD specimens to the predefined Cervidae groups, we performed two sequential analyses. In the first, the two predefined groups were Muntiacinae and three-tined deer (Cervinae and Capreolinae), and all of the complete DD specimens were assigned to one of these groups.

Description

Cranial appendages

The collection of DD cranial appendage fragments does allow for a separation of large- and small-sized specimens. Moreover, clear morphological differences in the large specimens point to two different morphotypes (Figs. 2 and 3).

Large pedicles morphotype 1

The postorbitally placed pedicles are moderately long ($1.5 < L/DTW < 3.0$) (see appendix, Table 2), backwardly inclined and set partially on the cranial cavity. Rostrally, they merge into strong lateral ridges of the frontals, forming thickened dorsal orbital rims (Fig. 2, morphotype 1). Specimen DD 4981 (Fig. 2a, morphotype 1), which is the only specimen with a preserved sagittal suture, points to parallel orientation in the frontal view of both pedicles of one individual. The cross-section is approximately circular.

Large pedicles morphotype 2

The postorbitally placed pedicles are moderately long ($1.5 < H/DTW < 3.0$) (see appendix, Table 2), greatly inclined backwards and set partially on the cranial cavity (Fig. 2a, morphotype 2). The orientation of a pair of these pedicles to one another in an individual in frontal view, either parallel or divergent, is unknown, since none of the specimens has a preserved sagittal suture. The pedicle is compressed longitudinally at the basis, and it is not prolonged with a ridge at the side of the forehead (the orbital rim is thin) (Fig. 2, b, c, morphotype 2). The cross-section is almost circular under the coronet.

Small pedicles

The pedicles are very small, but moderately long ($1.5 < H/DTW < 3.0$) (see appendix, Table 2) and placed supraorbitally with a slight inclination backwards. Since specimen DD 519 bends slightly to medial, this might indicate a convergent orientation of the pedicles of one individual (Fig. 4b) in frontal view. The cross-section is oval, being largest at the antero-posterior axis, or approximately circular. The pedicles do not show evidence of merging into lateral ridges at the frontals (Fig. 4b). We cannot discard completely the possibility that they represent very young specimens (fawns of *Capreolus* and those of some other cervids can early develop very tiny pedicles with "infant antlers"; Whitehead 1993).

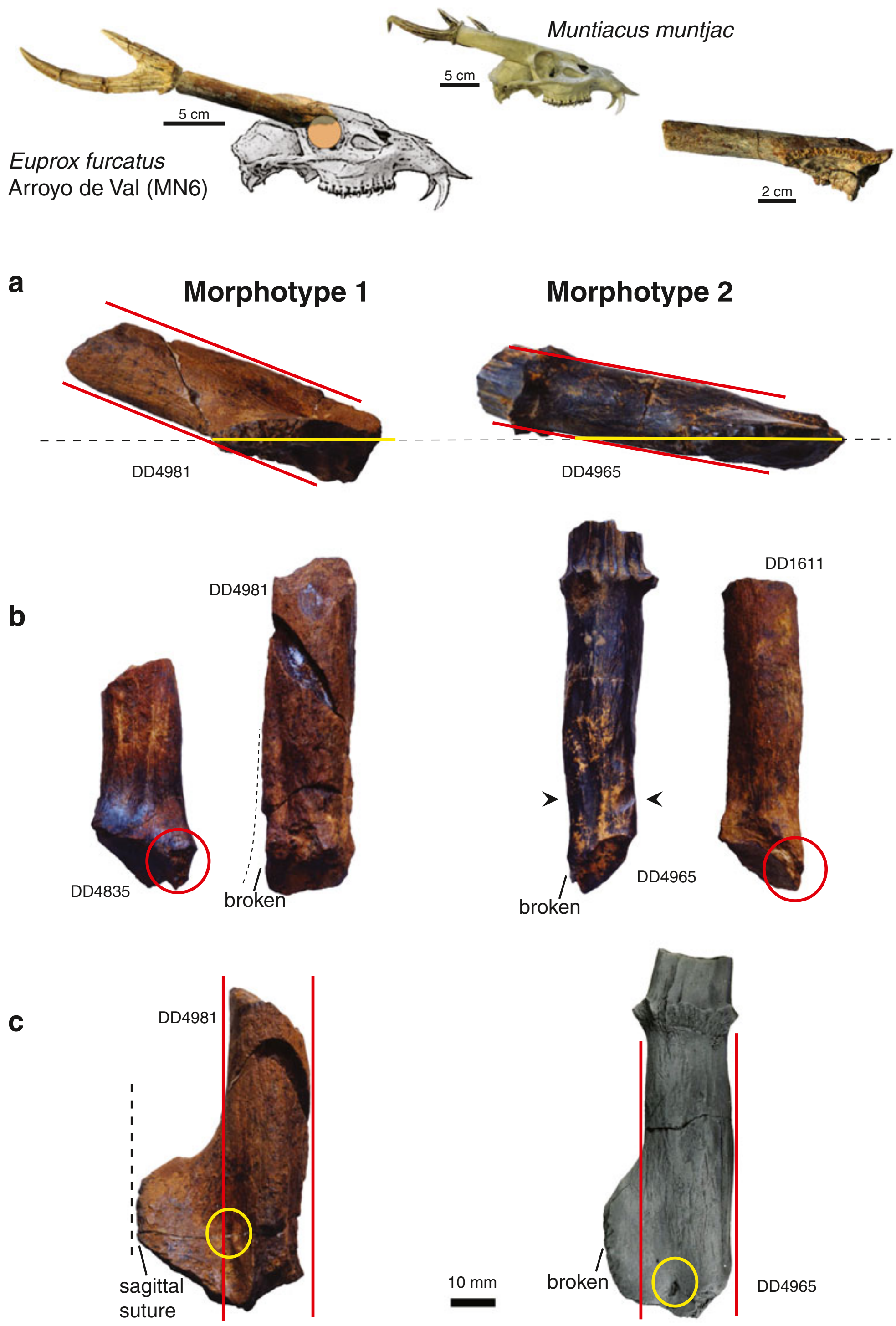


Fig. 2 Large pedicle morphotypes. **a** Medial view. The specimens are rotated to coincide the frontal with the horizontal plane. The inclination is estimated by the angle between the horizontal and the longitudinal axis of the pedicle. Morphotype 2 has a greater inclination backwards, as in living and fossil (*Euprox furcatus*) muntiacines (*above*). **b** Lateral view. Pedicle of morphotype 2 is compressed at the basis (*arrowheads*), and the orbital rim (*red circles*) is thinner than that of morphotype 1. **c** Frontal view. In morphotype 1 the pedicle is oriented in parallel to the sagittal suture (in morphotype 2 it is unknown), and the fossa (*yellow circles*) for the foramen supraorbitale is placed more medially with respect to the pedicle

Large antlers

The antlers are very fragmentary, so the reconstruction of the complete morphology is a very difficult task. The differentiation in two morphotypes seems subtler than for the pedicles.

Large antlers morphotype A: two-tined or three-tined (Fig. 3a–f)

The coronet is generally well developed and placed in a plane that slopes slightly downwards towards the medial side. The differentiation between tine and beam is very

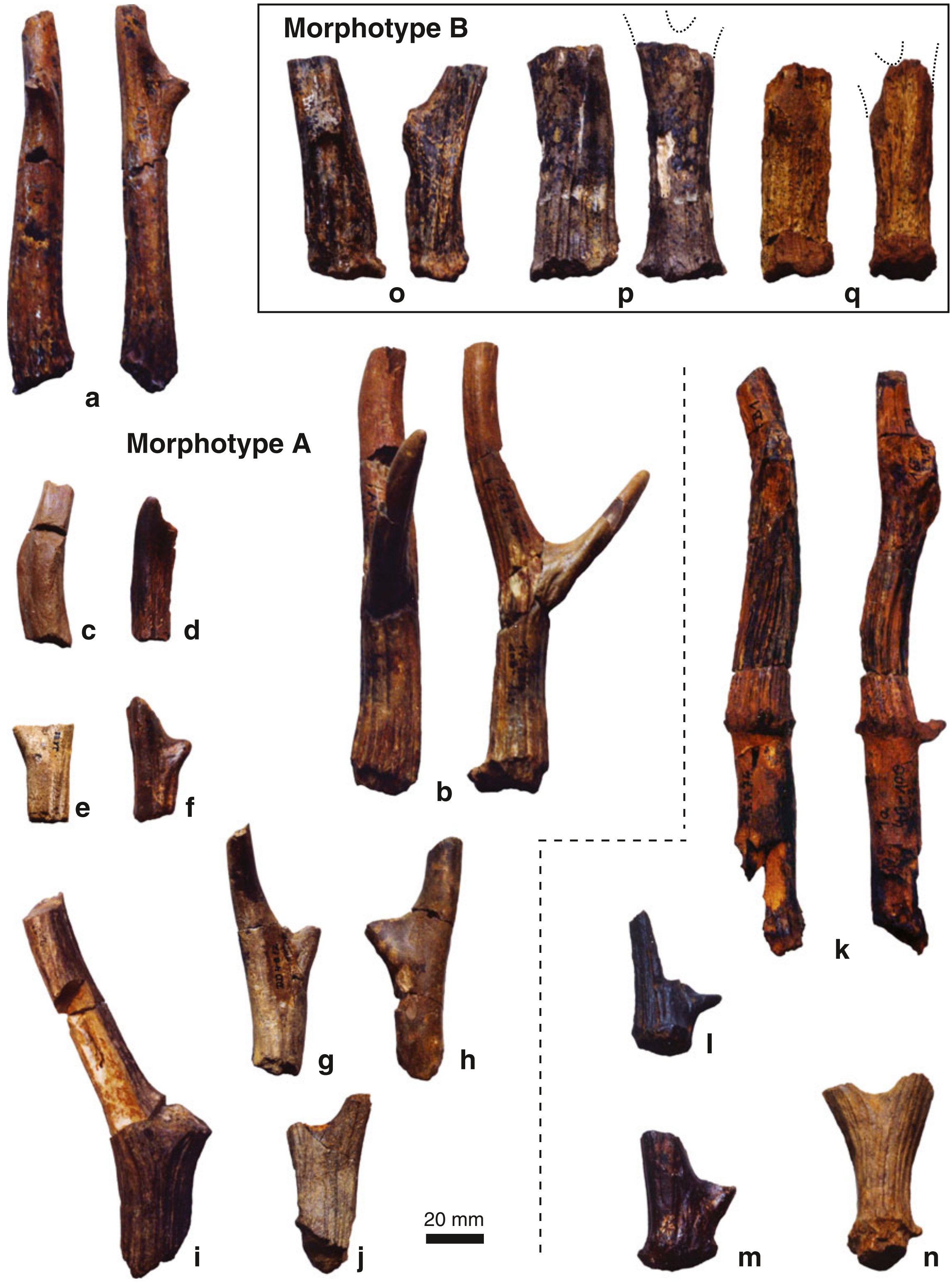
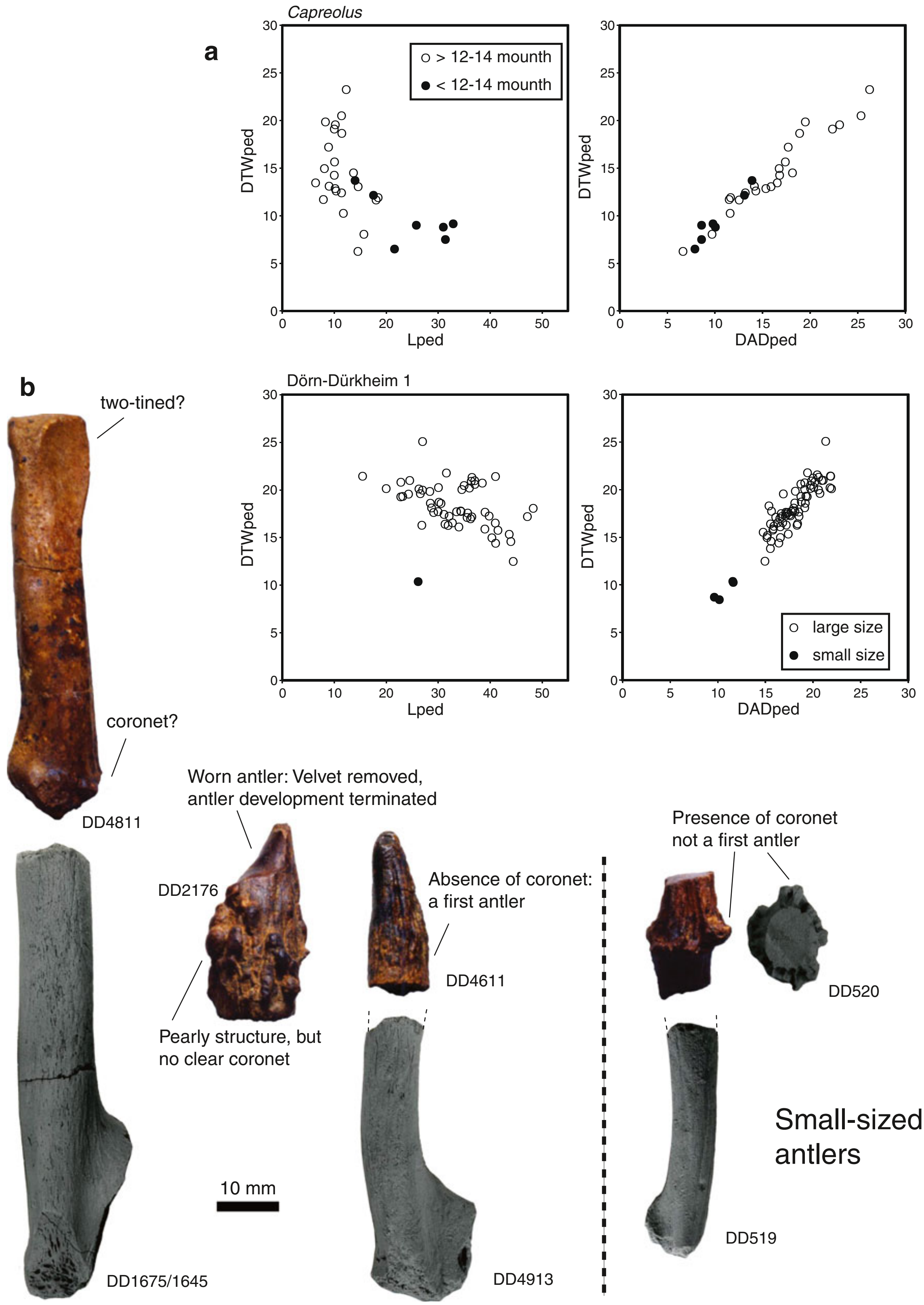


Fig. 3 Large antler morphotypes. **a**–**j** Morphotype A, **o**–**q** Morphotype B, **k**–**n** "Outliers". **a** DD4810, juvenile specimen, medial (*right*) and frontal (*left*) views. **b** DD 2896, adult specimen, medial (*right*) and frontal (*left*) views. **c**–**h** Possible second tines: **c** DD 4877 (lateral? view), **d** DD without number (medial? view), **e** DD 2198 (lateral/medial view), **f** DD 4563 (lateral/medial view), **g** DD 4812 (medial? view), **h** DD 4360 (lateral/medial view). **i** DD 2131, adult specimen, the preserved part of the intermediate beam portion (Ibp) is very long, and its distal section has a similar size as the section below the bifurcation in specimens of figures **g**–**h** lateral view. **j** DD 4603, second bifurcation?, lateral/medial view. **k** DD 2975–5774, basal beam portion (Bbp) bends to caudal, medial (*right*) and frontal (*left*) views. **l**–**m** Antlers with a basal accessory tine: **l** DD 4813, **m** DD 4931, lateral/medial view. **n** DD 4824, short Bbp showing a rather dichotomous construction (lateral/medial view). **o** DD without number, medial (*right*) and frontal (*left*) views. **p** DD 2129 medial (*right*) and frontal (*left*) views. **q** DD 2155, medial (*right*) and frontal (*left*) views



well established (monopodial construction). The beam cross-section starts either roughly circular or oval, with the major axis oriented more or less perpendicularly to the plane of the bifurcation. Some slender specimens (juvenile?) exhibit a medial keel. In frontal view, the beam bends gently to medial somewhat higher from the burr,

◀ **Fig. 4** **a** Pedicle (*ped*) variability of Dorn-Dürkheim 1 (DD) sample compared to the ontogenetical variability in extant *Capreolus*, documenting most likely two species. DD pedicles exhibit a larger variability than those of the *Capreolus* sample, which is constituted mostly by *C. capreolus,* but the biggest specimens could correspond to *C. pygargus.* Dimensions in millimetres. **b** Small cranial appendages (*right*) compared with possible juvenile specimens of large appendages (*left*). *L* Length, *DTW* Distal transversal width, *DAD* distal anteroposterior depth

i.e. it is slightly s-shaped having formed a lyriform pair of antlers in the lifetime of the animals. In lateral view, the beam shows a slight posterior inflexion at the bifurcation level. Although none of the specimens comprises or evidences two bifurcations, specimens DD 4812 (Fig. 3g), 4563 (Fig. 3f), 4360 (Fig. 3h) and 4892 are small fragments just broken below a bifurcation, with the beam and tine pointing from this being very slender. Also, specimen DD 4877 (Fig. 3c) and another unnumbered specimen (Fig. 3d) are apices with an incipient offshoot. All could correspond to a second bifurcation, but we cannot exclude the possibility that they are juvenile. The first tine is set very high above the coronet and points from the anterior margin of the beam at an acute angle (35–45°). The second tine, if it exists, points far from the first one (the preserved portion of the Ibp in DD 2131 (Fig. 3i) and 2896 (Fig.3b), is 82 and 78 mm, respectively).

Large antlers morphotype B: dichotomous or two-tined (Fig. 3o–q)

The coronet is generally well developed and placed in a plane that slopes slightly downwards towards the medial side. There is no clear differentiation into tine and beam; some specimens are clearly dichotomous. The shaft is strongly compressed longitudinally (cross-section roughly oval with the major axis oriented more or less perpendicularly to the plane of the bifurcation) with keels that can be strong medially. In frontal view, the shaft bends slightly from the burr to lateral (which could indicate a gently medial curve in a complete antler), i.e. antler pairs were not lyriform. The branches/tines are not preserved.

Small antlers (Fig. 4b)

Specimens DD 520 and one without number are the most complete small antlers, but both have only a very short antler portion preserved that is attached to the distal portion of the pedicle (about 1 cm above the coronet). No indication of a basal branch or tine exists, and the basal cross-section follows that of pedicles and is oval. There is a coronet, and the morphology does not seem to be conic, so these specimens are not first-year antlers (fawns of *Capreolus* can develop very tiny button antlers or "infant antlers" very early and these can be shed and re-grow again during the first year, i.e. before the first head grows in the second year; Whitehead, 1993). By contrast, specimens DD 4816 and DD 1876 are very tiny spike antlers without a clear coronet and dimensions close to those of the distal part of pedicle DD 519. The overall morphological pattern of the antler is unknown.

Dentition

Large dentition [Figs. 5, 6; see appendix, Tables 3, 4; Electronic Supplementary Material (ESM) 1–4]

The large dentition is brachyodont but shows an incipient tooth crown height increase (0.9 < H/W < 1.2 of unworn m3) and exhibits an advanced stage of premolar molarisation. Some enlarged upper canines show the typical sabre-shaped morphology of middle Miocene deer (e.g. Fig. 5a) with a slight s-shape in anterior view. All upper premolars have a rounded lingual shape and a pronounced labial column of the anterolabial cone. The size of the latter decreases significantly from P2 to P4. The anterior style is always well developed. From P2 to P4 the distance between the anterior style and the labial column of the anterolabial cone increases and the posterolabial crista becomes shorter. A weaker posterolabial cone is more or less developed on P2s and P3s. All premolars display molarisation with a second lingual cone, of which the anterior is the less pronounced of the two. The medium worn P4 specimen DD 4763 (Fig. 5f) clearly shows separation between both cones by enamel layers—at least at this stage of wear. Fusion below cannot be excluded, but is not clearly to be seen. One or two central folds originate at the posterolingual cone with the direction towards the anterolingual cone. Specimen DD 1047 even has a third central fold with its origin at the anterolingual cone and orientation towards the anterolingual cone. A weak cingulum surrounds the lingual part of the basis of P4s.

Upper molars have a pronounced paracone, parastyle and mesostyle. The labial column of the metacone and metastyle is weak. Postparacrista, premetacrista, external postprotocrista and premetaconulecrista are unfused in early wear. The internal postprotocrista (central fold in Azanza 2000, but "aile postérieure du protocone" in Heintz 1970) is always strong, but increases significantly from M1 to M3. It is oriented transversally or parallel to the premetaconulecrista in M1s, but in M2s and M3s it originates from the middle part of the protocone, with an orientation towards the join between postparacrista and premetacrista, The external postprotocrista (postprotocrista in Azanza 2000, but "pli protoconal" in Heintz 1970) is

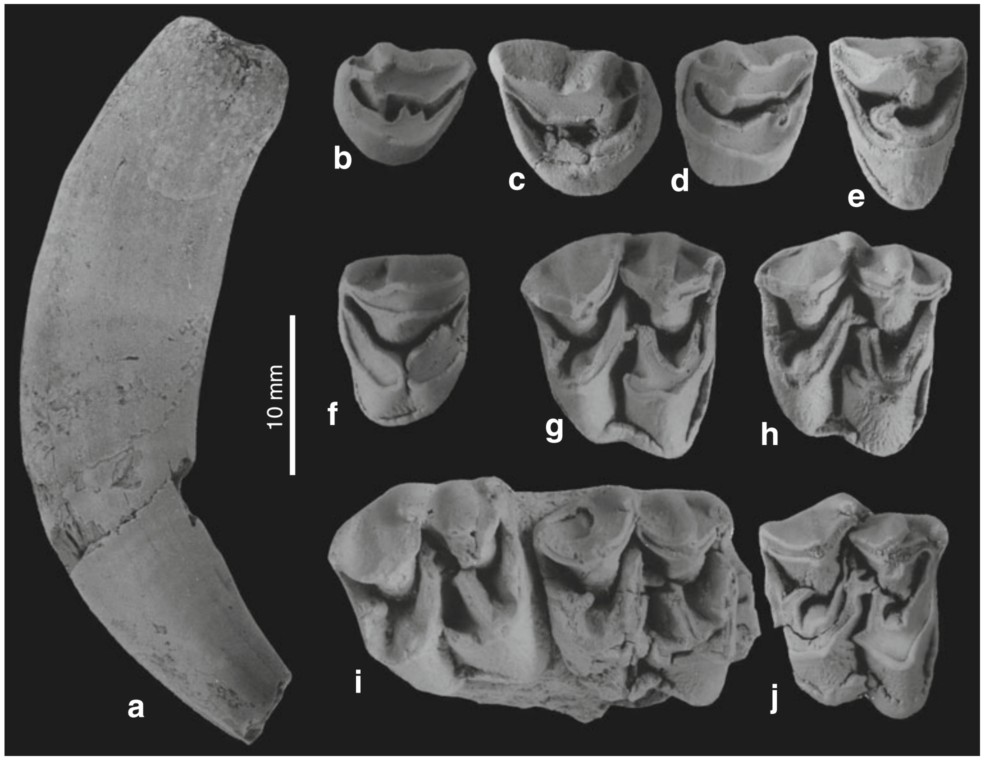


Fig. 5 Large upper teeth. **a** Left canine, DD 1333, labial view. **b** Left P2, DD 1069, occlusal view. **c** Right P2, DD 1030, occlusal view. **d** Left P3, DD 1018, occlusal view. **e** Right P4, DD 1044, occlusal view. **f** Left P4, DD 4763, occlusal view. **g** Right M3, DD 843, occlusal view. **h** Right M3, DD 806, occlusal view. **i** Fragment of right maxillary with M2 and M3, DD 4793, occlusal view. **j** Right M1, DD 843, occlusal view

always present and oriented towards the metaconule, but very weak at an advanced stage of wear. Small accessory folds are common in premetaconulecrista and in external postprotocrista, and frequently one of these originates anterior of the lingual end of the premetaconulecrista and is directed towards the internal postprotocrista. Sometimes both cristae are fused. A short, but pronounced metaconule fold is present in most upper molars. A more or less developed cingulum is present, and an entostyle can emerge from the lingual one.

The lower premolars exhibit an advanced molarisation as well. The transverse cristid is generally strongly backwards oriented. The anterior stylid and anterior conid are clearly developed. Specimen DD 1236 (Fig. 6e) is a right jaw fragment with p4 and p3, which helps to differentiate the morphology of both tooth positions. This specimen documents a similar morphology in both teeth, with pronounced mesolingual conid and posterolingual cristid as well as clearly developed anterior stylid and anterior conid. The anterolabial cristid is bent to lingual and gives the teeth a blunt anterior end. Posterior cristid and posterior stylid fuse in a lower level. The mesolingual conid is much stronger in the p4 than in the p3 and is also more anteriorly positioned. Sometimes the anterolingual cristid is developed and nearly closes the anterior valley by ending close to the anterior conid (DD 1310; Fig. 6d) or to the anterior stylid (DD 1316; Fig. 6c). In these specimens the anterior conid is very tiny. In other p4s the posterolingual conid-complex is often isolated. The posterolabial conid is extremely pronounced in p4s with a marked labial incision. Specimen DD 1267 is a right jaw fragment with a p3 and alveols of a p2. The p3 fits in size and morphology with other large p3s. p2s have a weak mesolingual conid and no anterior stylid. The anterolabial cristid is directed towards the anterior. The overall shape of p4s is compact triangular, with the acute angle oriented to the anterior. p3s are more slender, and p2s are even more slender than p3s with a less blunt anterior tip.

Lower large molars exhibit a clear labial column for the metaconid, entoconid and metastylid. The cristids are unfused in early wear. The metaconid-complex and entoconid-complex are not in line, but in parallel to one another with a slightly inclined orientation to the tooth axis. The ectostylid is pronounced. Anterior and posterior cingulids are weak. An external postprotocristid (*Palaeomeryx*-fold) is weak or absent. The third lobe of the m3s is small and placed centrally to the tooth axis. The hypoconulid of the m3 is oriented to the labial. The back fossa of the m3 is predominantly surrounded by the hypoconulid-complex. The entoconulid is weak and isolated in early wear. As it is placed more labially than entoconid, the lingual wall shows a sharp inflexion. Specimen DD 1199 (Fig. 6h) is a right jaw fragment with m3 and m2, which corresponds in size to the largest isolated lower molars.

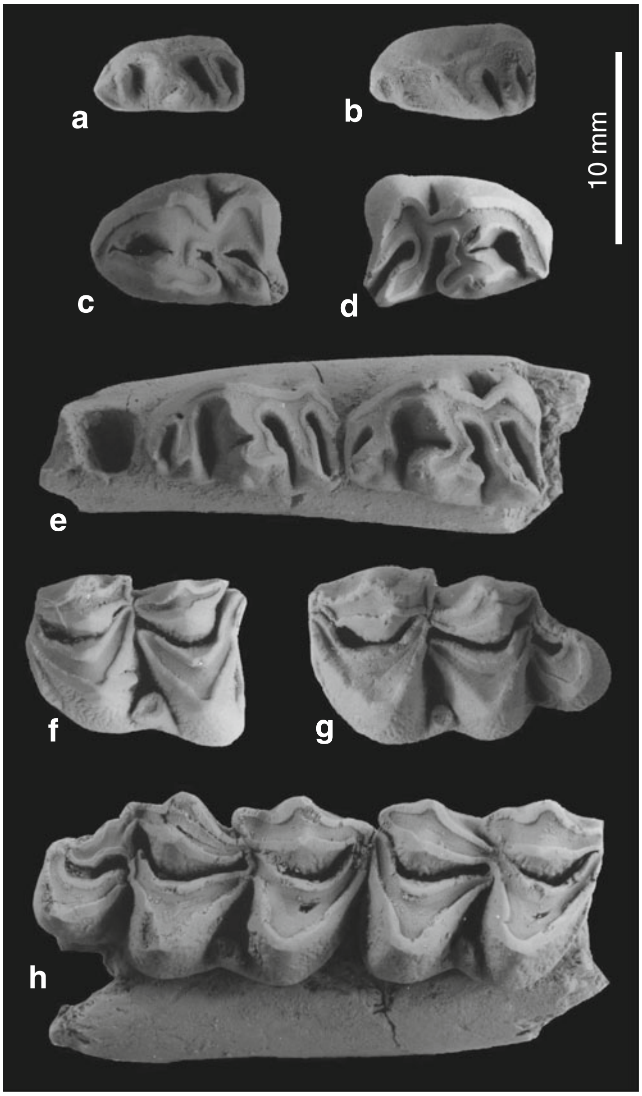


Fig. 6 Large lower postcanine teeth. Occlusal views. **a** Right p2, DD 1251. **b** Right p2, DD-1270. **c** Right p4, DD 1316. **d** Left p4, DD 1310. **e** Fragment of right mandible with p3–p4. DD 1236. **f** Left m1, DD 1151. **g** Left m3, DD 4794. **h** Fragment of right mandible with m2–m3, DD 1199

Small dentition (Fig. 7; see appendix, Tables 3, 4; ESM 1–4)

The small dentition is also brachyodont and exhibits a similar grade of hypsodonty (H/W = 1.01 in the only unworn m3 DD 4674), but fewer molarised premolars than the large dentition. All upper premolars have a semi-elliptic lingual shape. The labial column of the anterolabial cone is pronounced and can be flattened towards the anterior. The anterior style is always well developed. A weak posterolabial cone is developed on P2s and P3s. Some premolars display a low degree of molarisation with a weak labial incision separating a tiny second lingual cone. A central fold, backwardly oriented, can originate at the posterolingual cone. The cingulum is very weak or absent.

Upper molars have a pronounced paracone, parastyle and mesostyle. The labial column of the metacone and the metastyle is weak. The cones are comparably more rounded and the cristae less developed than in the large dentition. Postparacrista, premetacrista, external postprotocrista and premetaconulecrista are unfused in early wear. The internal postprotocrista (central fold in Azanza 2000, but "aile postérieure du protocone" in Heintz 1970) originates posteriorly to the protocone and is oriented transversally or parallel to premetaconulecrista. The external postprotocrista (postprotocrista in Azanza 2000, but "pli protoconal" in Heintz 1970) is short and frequently absent at a moderate stage of wear. Small accessory folds are rare in premetaconulecrista. A short, but pronounced metaconule fold is present in some upper molars. Cingula are very weak or can be absent. Entostyles are always present, but can be weak.

The lower premolars also exhibit a less advanced molarisation than in the large dentition. The transverse cristid is generally strongly backwards oriented. The anterior stylid is more developed than the anterior conid and in p2s it is oriented towards anterior. The anterolabial cristid is shorter and more bent to lingual from p2 to p4. p4s have a pronounced mesolingual conid and posterolingual cristid as well as a clearly developed anterior stylid and anterior conid. There is no anterolingual cristid, but in a p4 (DD 4042; Fig. 7d) the mesolingual conid nearly closes the anterior valley by ending close to the anterior conid at a low crown level. In this specimen the posterolabial conid is extremely pronounced with a marked labial keel. The anterolabial and posterolabial cingulids are strong in p4s. The posterior cristid and posterior stylid fuse at a low crown level. The overall shape of p4s is roughly trapezoidal, with the shortest side oriented to the anterior, forming a blunt anterior tip. p3s are more slender and p2s are even more slender than p3s, with a sharp anterior tip.

Lower molars exhibit a clear labial column for the mesostylid, metaconid, metastylid and entoconid. The cristids are unfused in early wear and comparably shorter than in the large dentition. The metaconid-complex and entoconid-complex are not in line, but in parallel to one another with a slightly inclined orientation to the tooth axis. The ectostylid is weak. Anterior and posterior cingulids are pronounced. An external postprotocristid (*Palaeomeryx*-fold) is more or less developed. The posthypocristid is thin and elongated to join the postentocristid in m3 (DD 489; Fig. 7f). The third lobe of the m3s is big and placed labially to the tooth axis. The hypoconulid of the m3 is oriented

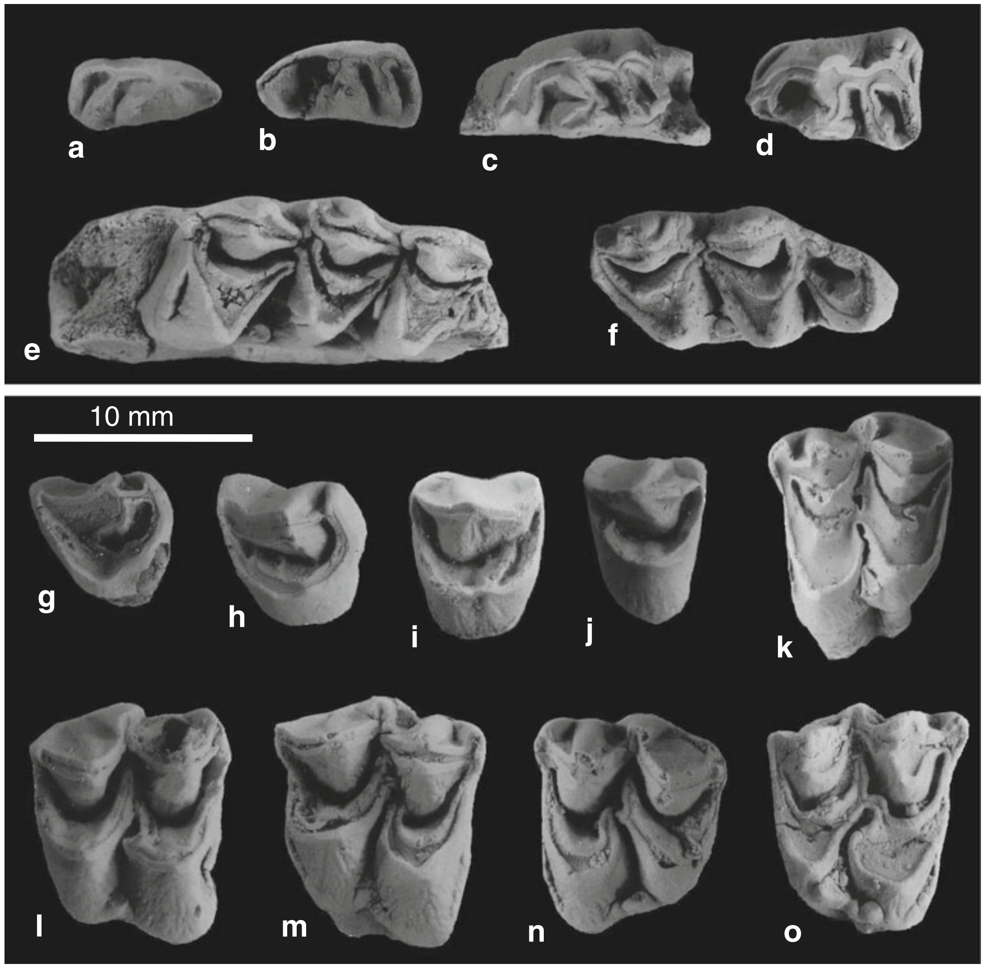


Fig. 7 Small postcanine dentition. Occlusal views. **a** Left p2, DD 512. **b** Right p3, DD 954. **c** Fragment of right mandible with p4, DD without number. **d** Right p4, DD 4042. **e** Fragment of right mandible with dp4 (*broken*) and m1, DD 1132. **f** Left m3, DD 489. **g** Right P2, DD without number. **h** Right P3, DD 1070. **i** Left P3, DD 950. **j** Right P4, DD 513. **k** Left M1, DD without number. **l** Right M2, DD 4100. **m** Right M2, DD 4729. **n** Left M3, DD 3807. **o** Right M3, DD 919

towards the labial. The back fossa of the m3 is nearly completely surrounded by the hypoconulid-complex. The entoconulid is very weak and isolated in early wear. It is placed more lingually than in the larger dentition, so the lingual wall describes a slight inflexion.

Morphometrical analyses

The fragmentary condition of DD cervid remains greatly hampers the possibility of taxonomic determination. Clear size classes in teeth are an appropriate first approach to species discrimination due to finished growth with terminated enamel cap development prior to tooth eruption. However, similar size classes in teeth of different species might derive from interspecific variation, intraspecific variation or sexual dimorphism. Tooth crown characters can help here to distinguish between species, but the absence of complete or more or less complete tooth rows do not allow premolar morphotypes and molar morphotypes to be associated. The morphology and size of antlers and pedicles are not only affected by lifelong growing due to the antler cycle, but also by a high variability, as known from antlers in extant cervids. Consequently, the association between corresponding teeth and cranial appendages and finally taxonomic assignment is another very difficult task. For that reason, the previous assignment (Franzen 1981; Franzen and Storch 1975, 1999) of DD cervid remains to a changing number of two or three species is a reproducible fact. Based on the following in-depth morphometrical analysis, we have achieved another modified result of the former three-species solution.

Bivariate plots of occlusal width versus occlusal length for all cheek teeth are provided in ESM 1–4. A clear separation in two sizes appears in all teeth. The teeth of the small-sized DD cervid is similar in size to those of the extant *Muntiacus reevesi*. They are comparable to the small dentitions assigned to *Cervavitulus mimus* (Piera, Aubignas I in Azanza et al. 1993) and also similar to those of *"Dremotherium" penteleci* of Pikermi (Fig. 8) (measurements in Azanza 1995), whose antlers are unknown. The small-sized DD cervid has only slightly smaller molars than *"Euprox" minimus* from Göriach and *"Paracervulus" australis* from Montpellier (Fig. 8). However, they are clearly smaller than those of *Amphiprox* of Can Llobateres, *Lucentia iberica* from Crevillente 2 and all three-tined cervids included in the analysis.

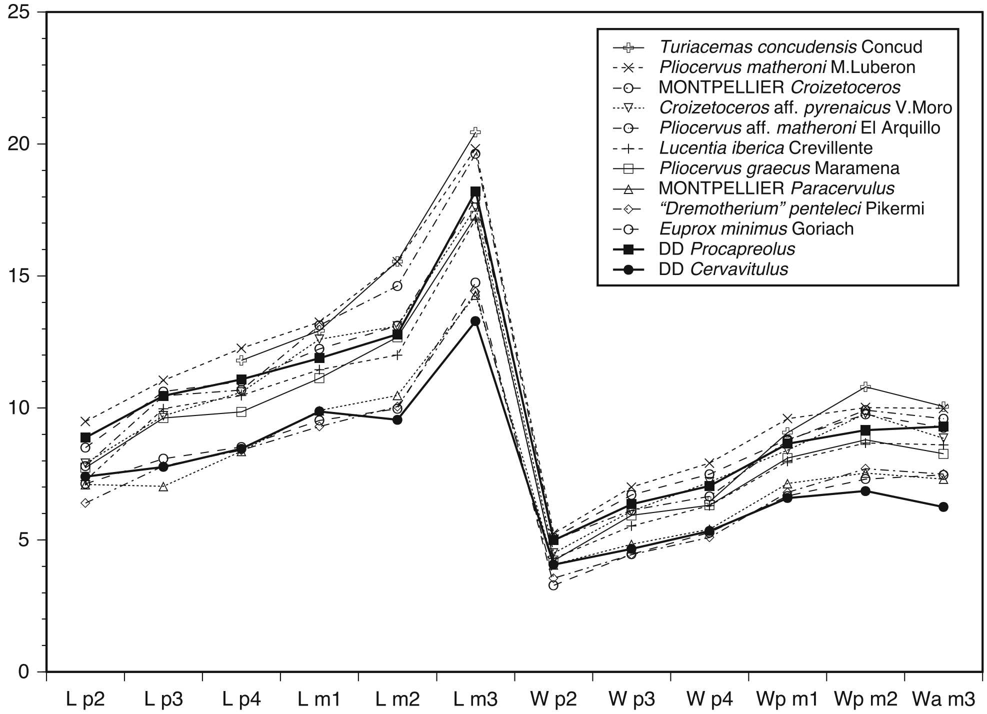


Fig. 8 Lower teeth size comparison between late Miocene and early Pliocene cervids. Dimensions are in millimetres

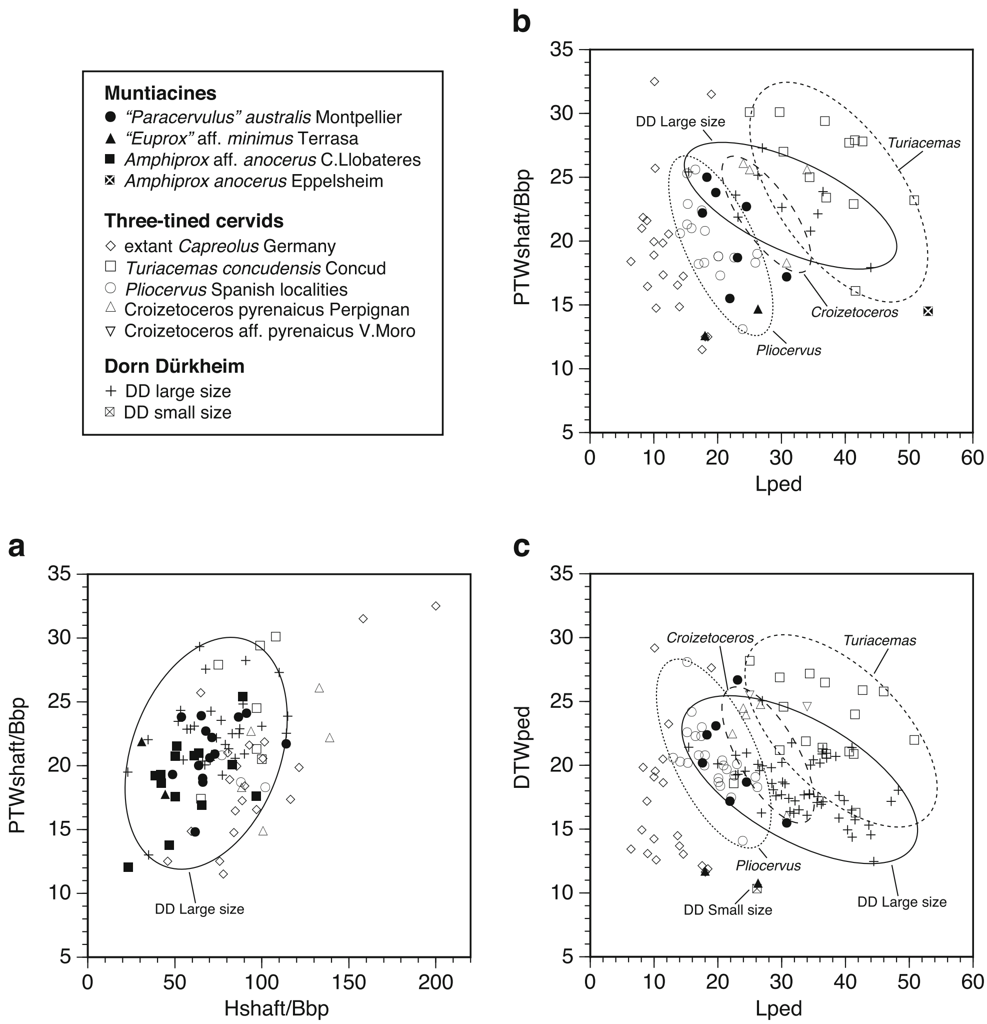
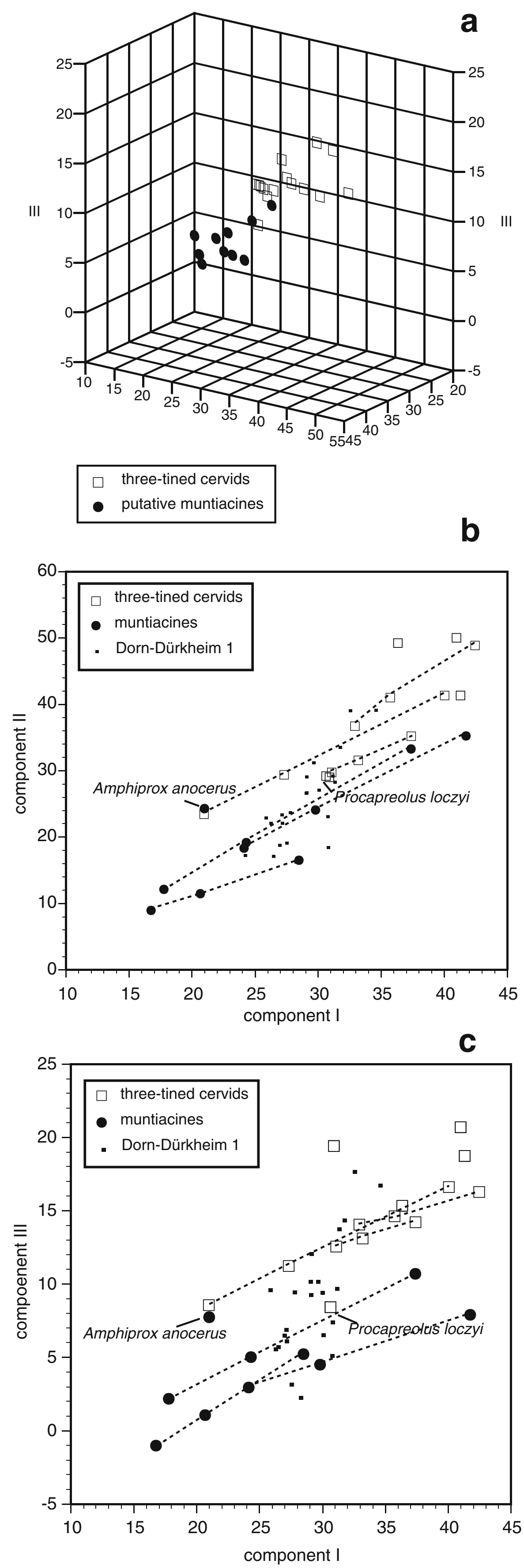


Fig. 9 Comparison between size and morphology of DD appendage specimens and those of European late Miocene muntiacines (*filled symbols*) and three-tined cervids (*open symbols*). Dimensions are given in millimetres. **a** Scatter plot of the height vs. the proximal transversal width of the shaft/Bbp. **b** Scatter plot of pedicle length vs. antler proximal transversal width of the shaft/Bbp. **c** Scatter plot of the length vs. the distal transversal width of the pedicle

Fig. 10 Result of the Principal Component Analysis using five variables measured on shaft/Bbp of the DD antler specimens and that of the European late Miocene muntiacines and three-tined cervids. **a** 3D scatter plot of the three first components that capture 94.03 % of the variability. **b** 2D scatter plot of the first (67.35 % of the variability) vs. the second (14 % of the variability) component. **c** 2D scatter plot of the first vs. the third (12.71 % of the variability) component



The variability in size and shape of the pedicles has been compared with the ontogenetical variability found in extant *Capreolus* (Fig. 4a). We measured the pedicles of 20 skulls of juvenile, adult and senile individuals of *C. capreolus*. The biggest ones could even correspond to *C. pygargus* since this species was introduced in Germany by hunters. The individual age has been estimated through stages of dental replacement and wear. Pedicles of juvenile (<12–14 months) *Capreolus* were significantly longer than those of adult/senile (>12–14 months) *Capreolus*, but both age groups overlap. Despite being slender, the pedicle of juvenile individuals is similar in distal proportions to that of adults/seniles. DD specimens are distributed again in two clearly separated size groups, but these groups do not follow the ontogenetical pattern of *Capreolus*, suggesting that they do not correspond to only one species. Moreover, it must be noted that the DD sample shows more variation in proportions than extant *Capreolus* (although there could be two species in the *Capreolus* sample).

The size and shape of the pedicle and shaft/Bbp of DD specimens are compared with those of the Western European late Miocene species and extant *Capreolus* in Fig. 9. Shaft/Bbp shape (Fig. 9a) does not allow late Miocene species to be discriminated, but it does suggest a certain segregation within muntiacines and three-tined cervids. Overall, DD specimens greatly overlap both groups. Figure 9b, c provides a bivariate plot of the pedicle length versus shaft/Bbp basal width (b) and pedicle distal width (c). Despite some overlap, these graphs clearly show the separation of size classes. DD large-sized specimens do not correspond to any known species (data for DD small-sized specimens, *Amphiprox* of Can Llobateres and *Procapreolus loczyi* are not available).

A PCA using the five measurements (see appendix, Table 2) of the shaft/Bbp (Fig. 10; see appendix, Table 2) evidence the separation between muntiacines and three-tined cervids. To simplify the analysis, data of each species are reduced to the sample mean and its lower and upper confidence limits for each measurement. The small overlap between both groups is due to the close position of the holotypes of *Amphiprox anocerus* and *Procapreolus loczyi*. However, DD specimens greatly overlap both groups, thereby confirming the notion that there are at least two species, one of them a muntiacine.

In order to evaluate the suitability of the sets of metric variables to distinguish the shaft/Bbp of muntiacines and three-tined cervids, we performed a discriminant analysis. The DD specimens were classified according to the model derived. Figure 11 displays the results obtained. There are more

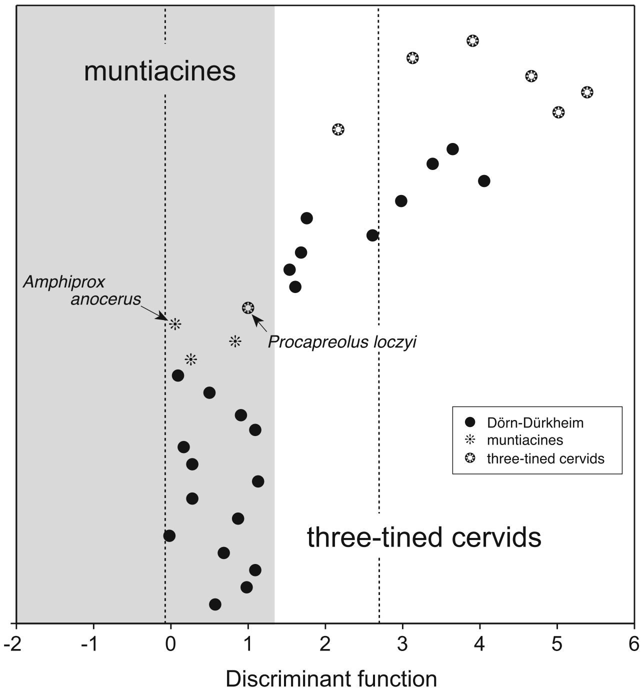


Fig. 11 Classification of the DD antler specimens according to the distribution model derived from the discriminant analysis using the five variables measured on the shaft/Bbp of the European late Miocene muntiacines and three-tined cervids. The *dotted lines* indicate the values of the group centroids in the discriminant function

specimens classified in the "muntiacines" than in the "three-tined cervids". However, it should be noted that the holotype of *Procapreolus loczyi* has been classified in the "muntiacines"; thus, it is not certain that all DD specimens classified as "muntiacines" actually belong to this classification.

Taxonomy

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Infraorder Pecora Linnaeus, 1758
Superfamily Cervoidea Goldfuss, 1820
Family Cervidae Goldfuss, 1820
Subfamily Capreolinae Brookes, 1898
Tribe Capreolini Brookes, 1898
Genus *Procapreolus* Schlosser, 1924
Type species *Procapreolus latifrons* Schlosser, 1924

Procapreolus sp.

Hypothesis 1: Morphotype 1? + morphotype A + large dentition (in part)

Hypothesis 2: Morphotype 1? + small pedicles + morphotype A + small antlers + large dentition (complete)

Comparisons: The possible three-tined antlers of morphotype A correspond to a common Turolian pattern with the first tine set high above the coronet. However, the Bbp is longer and more slender than in adult antlers of *Cervavitus* or *Pavlodaria*, but not as long as in *Lucentia iberica*, *Pliocervus*, *Turiacemas*, *Croizetoceros pyrenaicus* and some *Procapreolus* species (*P. cusanus*, *P. ucrainicus*, *P. florovi*, or *P. moldavicus)*. The beam can be somewhat s-shaped and is longitudinally compressed along the Bbp and, at least, the proximal part of the Ibp. This general Bbp morphology is closer to that of *Procapreolus loczyi* from Polgardi (MN12; Hungary), but the beam is less compressed longitudinally and shows weaker posterior inflexion at the first bifurcation level, and the Ibp (if the second bifurcation exists) is longer. According to Vislobokova (2007), *Procapreolus* aff. *loczyi* from Kohfidisch (Austria) has lyriform pairs of antlers with a high position of the first tine, but they differ from the antlers of *P. loczyi* in their smaller size and in the absence of the second bifurcation, possibly because of a younger individual age of the animals. Despite none of the DD specimens shows two bifurcations, several beam fragments could correspond to a second bifurcation from which a weak tine develops (see above).

The diagnosis for *Procapreolus* is based on the antler reconstructon of *Procapreolus latifrons* from Mongolia (Schlosser 1924) and China (Zdansky 1925). The clearly parallel pedicles and slightly half-lyriform beams are considered typical for *Procapreolus* according to Korotkevich (1965); nevertheless, the type species *Procapreolus latifrons* from Mongolia (Schlosser 1924) and China (Zdansky 1925) does not exhibit the second feature. Other species attributed to *Procapreolus* (*P. cusanus*, *P. moldavicus*) do not share the parallel pedicles. The pedicles of the two specimens attributed to *P. florovi* and figured by Korotkevich (1974) have different morphologies: one has parallel, closely positioned pedicles, while the other has very divergent and less closely positioned pedicles. In extant *Capreolus*, the antlers can be lyriform or straight forming a V. *Capreolus capreolus* has parallel, closely positioned pedicles, but the bigger *C. pygargus* has somewhat divergent pedicles. Thus, these features differ at species level.

None of the DD specimens gives a hint which of the two large pedicle morphotypes has been associated with the large antler morphotype A. However, we consider morphotype 1 to be the most probable because these pedicles are oriented in parallel to the sagittal plane (see above). Moreover, they merge rostrally into strong lateral ridges of the frontals to form thickened dorsal orbital rims. The holotype of *Procapreolus loczyi* is a cast antler. None of the other antlers that have been reported to this species from Hungary, Serbia and Austria have an attached pedicle, but some isolated pedicles have been assigned to this species. All of them seem to merge into lateral ridges at the frontals according to the figures. Also, this feature is noted for an isolated pedicle assigned to *P.* cf. *loczyi* from Baccinello V3 (Abbazzi 2001); however, the orientation in this specimen is slightly divergent to the sagittal plane. Other *Procapreolus* species do not share this feature—the orbital rim being thin and protruding from the lateral side of the pedicle. The proportions of the DD pedicles are clearly different from those of *Lucentia*, *Pliocervus*, *Turiacemas* and *Croizetoceros* (Fig. 9).

According to size classes represented in DD cranial appendages and DD teeth we associate large-sized teeth with antler morphotypes A and B and with pedicle morphotypes 1 and 2 (hypothesis 1). Although there is some variability, we are not able to detect two distinct groups, either morphologically or metrically, based on isolated teeth. The upper molars retain a strong internal postprotocrista and the lower molars a variously developed external postprotocristid. Upper canines are moderately long. The premolars are strongly molarised, the P4 can be bilobed with a deep lingual groove and p4 shows a very well-developed anterolingual cristid. This combination of features is present in *P. loczyi*, *P. ucrainicus* and *P. moldavicus*. Other Turolian deer (*Lucentia*, *Turiacemas*, *Pliocervus* and *Croizetoceros*) have both internal postprotocrista and external postprotocristid reduced or even completely absent.

One crucial issue to solve the extent of the taxonomical diversity of DD specimens, either to two or three species, is the interpretation of the small antlers and pedicles being either first cranial appendages of *Procapreolus* or regular antlers of a smaller-sized cervid. Hypothesis 2 considers this possibility. It is founded in the fact that fawns of *Capreolus* can develop early tiny button antlers or "infant antlers" (Whitehead 1993). The morphometrical analysis revealed that DD specimens do not follow the ontogenetical pattern of extant *Capreolus* and show even more variation in proportions. Consequently, we consider this hypothesis to be less plausible.

Subfamily Muntiacinae Knottnerus-Meyer, 1907

Muntiacinae gen. and sp. indet.

Hypothesis 1: Morphotype 2? + morphotype B + large dentition (in part)

Hypothesis 2: Morphotype 2? + morphotype B + small dentition?)

Comparisons: Franzen and Storch (1975) listed the presence of the muntiacine *Amphiprox anocerus*, but later this taxon was excluded from the DD taxonomical list. *Amphiprox anocerus* was described on the basis of a single specimen from the upper Miocene (MN9) of Eppelsheim (Germany) by Kaup (1839), who also described *Euprox dicranocerus* from the same locality. Some authors considered both species as synonymous and, consequently, they refused to consider *Amphiprox* as a valid genus (Gentry 2005). However, in the Spanish fossil record all cervid specimens from the earliest MN 9 (local zone H) are dichotomous, and the shaft is short as in *E. dicranocerus* holotype, while the *Amphiprox* morphotype with a long shaft is common in the latest MN9 (local zone I) localities, indicating the validity of both taxa (Azanza 2000; Azanza et al 1989, 1990). Böhme et al. (2012) as well as Pickford and Pourabrishami (2013, this issue) provide evidence of the stratigraphic inhomogenity of the fossil associations coming from several localities of the Eppelsheim Formation, which documents a reworking from early middle Miocene sediments. The *Amphiprox* morphotype is abundant in Can Llobateres, but there is as well great variability represented in this material, as seems to be the rule in Muntiacinae (Groves and Grubb 1990). There are specimens with high and low splitting while the trend toward the formation of a beam is developed to various degrees. Antler morphotype B is coherent with the diagnosis of *Amphiprox*. The morphometrical analysis reveals the excessive variability of the DD large appendage sample and corroborates the notion that there are two species, one of them a muntiacine (see above). The pedicle basis and the frontal bone of *Amphiprox* are unknown. The most plausible association with antler morphotype B is the pedicle morphotype 2. These pedicles are very strongly inclined posteriorly, and the frontals are very flat. This morphology is coherent with the definition of Muntiacinae of Azanza (1993).

In hypothesis 1 we also associated appendage morphotypes 2 and B with the large dentition. Vallesian muntiacines also present the combination of dental characters signalled previously for the large dentition, but the teeth are more brachyodont. However, there is no clear correspondence between antler size and teeth sizes in muntiacines. Thus, some species (*Paracervulus australis*, "*Euprox*" aff. *minimus* from Terrassa) have small teeth (of a similar size as the DD small dentition), but relatively large adult antlers (of a comparable size to the antlers of morphotype B). An association of antler morphotype B with the small dentition could be also plausible (hypothesis 2).

Subfamily *Incertae sedi*s

Genus *Cervavitulus* Kretzoi, 1951 (Actually a *nomen nudum* since figures were never published)

cf. *Cervavitulus mimus* Kretzoi, 1951

Hypothesis 1: Small pedicles + small antlers + small dentition?

Comparisons: Franzen and Storch (1975) assigned the small species of Dorn-Dürkheim to *Cervavitulus mimus* Kretzoi, 1951 from Csákvár (Hungary). The holotype from Csákvár V.11298, according to the photographs kindly made available by L. Kordos, has a size and a morphology close to that of DD 520, but the entire pedicle is preserved. It is slender, moderately long and strongly compressed transversally. It is only slightly set on the cranial cavity. The section is elliptic from its basis and the frontal is concave, so it seems possible that the pedicle was prolonged by a frontal crest. This morphology is common in Muntiacinae. This pedicle is very close to that of *"Euprox" minimus* from Göriach (MN5; Austria), but more slender and flattened. Although very scarcely represented, small cervid species seem to be common in the European lower Turolian localities. Azanza et al. (1993) included in *Cervavitulus mimus* certain teeth and postcranial elements from Aubignas I (MN11; France) and Piera (MN11; Spain). Also, the size of the small cervid *"Dremotherium" penteleci* of Pikermi (MN12; Greece) (Azanza 1995) is comparable, but some morphological differences exist (Azanza et al. 1993) that justify their specifical, or even generical, separation. No appendage specimens have been found in any of these localities that are comparable to the DD small pedicles and antlers. The DD small dentition is only slightly smaller than that of *"Paracervulus" australis* from the French Pliocene. A muntiacine form, referred to "*Euprox*" *minimus* (Azanza and Menéndez 1990), found in the Spanish locality of Terrassa (MN10) also shows a similar dental size. But both species have large adult antlers. However, the DD sample is so scarce and fragmentary that it is not possible to arrive at a definite decision on the taxonomical adscription of the small-sized dentition.

Discussion

Cervid remains from the fossil site of Dorn-Dürkheim 1 in Germany provide essential evidence for the discussion on the origin of crown cervids. Since these remains represent not only a further record of the only scarcely known early late Miocene cervid fauna, but also of a geographically underrepresented area, their investigation leads to a more complete picture of this phase of cervid evolution.

The classification of crown cervids

Traditionally up to seven subfamilies have been recognised for crown cervids because the peculiarities of four genera (*Capreolus*, *Hydropotes*, *Alces* and *Rangifer*) support those authors who want to classify them in their own tribes alongside Cervini, Odocoileini and Muntiacini. However, morphological (Bouvrain et al. 1989; Groves and Grubb 1987) and molecular studies (Hassanin et al. 2012; Gilbert et al. 2006; Pitra et al. 2004; among others) point to a main split between crown cervids that coincides with the two groups established by Brooke (1878): Plesiometacarpalia or cervids retaining only the proximal portion of their reduced second and fourth metacarpal, in contrast to Telemetacarpalia or cervids retaining only the distal portions. Thus, in classifications (see for instance Groves and Grubb 2011) only two subfamilies have been recognised, each with a subdivision into tribes: Cervinae (Tribes Muntiacini and Cervini) and Capreolinae [Tribes Alceini, Capreolini and Rangiferini (= Odocoileini)].

Contradicting hypotheses on cervid cladogenesis and the contextual importance of muntiacines

In general early late Miocene cervids take an interesting transitional position between crown cervids and early ancestors. The extant members are the second most diverse large herbivorous mammal group of the modern world after the members of Bovidae (antelopes, cattle, goats). With more than 50 species, they exhibit a wide range of adaptations to habitats in all biomes represented worldwide. Their ancestry can be traced back via fossils to the earliest cervids known from the early Miocene of Europe (Azanza 2000; Gentry 1994; Gentry et al. 1999; Obergfell 1957; Rössner 1995). With respect to the origin of crown cervids the early Turolian (European Land Mammal Mega-Zone of the early late Miocene) is a crucial time in the evolutionary history of Cervidae. Some middle Miocene cervids have been traditionally classified with the extant muntjacs and tufted deer (see, for instance, McKenna and Bell 1997), making the Muntiacinae the earliest of the modern subfamilies as well as the most primitive of extant antlered cervids (simple antlers and long pedicles and sabre-toothed upper canines, as well as their occurrence in tropical regions). As well as the above-mentioned characters they show others (very low chromosome number, absence of metatarsal glands, and the fact that in some species the antlers are only rarely cast) which suggest that they are descendants of Miocene cervids, not directly linked with other crown cervids (Bubenik 1990) and even deserving of family-level classification (Bubenik 1982, 1990; Groves and Grubb 1990). However the taxonomic status of extant muntiacines is controversial. Their plesiometacarpalian condition combines with recent molecular phylogenetic analyses (Gilbert et al. 2006; Hassanin et al. 2012; Kuznetsova et al. 2005; Pitra et al. 2004) to group them as a tribe within Cervinae.

The molecular divergence time between Cervinae and Capreolinae was calculated at between 11.5 and 7.7 Ma (Gilbert et al. 2006; Hassanin et al. 2012), and this would correspond to a time span in the early late Miocene from the early Vallesian to early Turolian European Land Mammal Mega-Zones, which the latter fits with subsequent dispersal data of Rangiferini (earliest appearance, latest Miocene, Vislobokova 1980; closure of Panama Isthmus, late Pliocene, Bartoli et al. 2005). According to Gilbert et al. (2006) this implies that (1) middle Miocene cervids cannot be included in the tribe Muntiacini and (2) the supposed primitive characters of muntiacines are in fact a derived condition.

However, this main split is not confirmed by the proposal of Marcot (2007) based on a supermatrix analysis of the entire artiodactyl clade (including whales) where muntiacines appear as sister group of the Cervinae + Capreolinae clade. This is in agreement with the proposal of Azanza (1993) and Azanza and Montoya (1995) based on fossil taxa and cranial appendage character evolution. In any case, the cladogenesis of crown cervids must have been gestated before the side metacarpal reduction to either the plesiometacarpal or telemetacarpal condition in the different lineages (Azanza and Montoya 1995). The youngest known record of a holometacarpal stage is *Cervavitus shanxius* (specimens figured in Zdansky 1925 and Teilhard de Chardin and Trassaert 1937, and reproduced in Dong 2011) from the late late Miocene of China (Henan and Shanxi provinces, Dong 2011). *Cervavitus* is considered to be a sister group of Cervini (see historical review of Pliocervini in Petronio et al. 2007) and, moreover, is one of the earliest cervids with the monopodial antler construction known from all crown cervids (see above). Further, it is associated in faunas with stem muntiacines (see above), which show synapomorphies in cranial appendages with living members of the tribe (Azanza 1993; Azanza and Montoya 1995). Oldest stem muntiacines (*Euprox*) are known from the middle Miocene, which in consequence is the minimum age of the origin of crown cervids.

This contradiction between the results of Gilbert et al. (2006) and Hassanin et al. (2012) has arisen because both those studies used as a calibration point in their molecular-dating calculations the oldest-known record of a muntiacine crown genus (*Muntiacus*, Dong et al. 2004) but ignored extinct muntiacine genera. We can see from a continuous fossil record that typically muntiacine cranial appendages, comprising postorbital backwardly-directed long pedicles and dichotomous antlers, together with elongated upper canines, cannot be considered to be derived (Gilbert et al. 2006; Groves 2007), but are ancestral features (Azanza 1993; Azanza and Montoya 1995). In contrast to the reconstructed ancestral character states in Gilbert et al. (2006) (three-tined antlers, large-sized, absent tusk-like upper canines), the fossil record also shows a different or even contrary pattern in character evolution (described above and in Gentry et al. 1999) for the last common ancestor of crown Cervidae, indicating a small-sized species with dichotomous antlers and enlarged upper canines.

Conclusions

Cervid antler and tooth remains recovered at the fossil site Dorn-Dürkheim 1 document three sympatric species, namely, *Procapreolus* sp., Muntiacinae gen. et sp. indet. and cf. *Cervavitulus mimus*. Their contemporary occurrence in the only Turolian fauna known from Germany is evidence of immigration of direct precursors of Capreolinae to the Western European realm, which overlapped with a resident distribution of the Muntiacini. Consequently, the Dorn-Dürkheim cervids complete the European picture of a progressive turnover of muntiacines and Capreolinae from Eastern to Western Europe during the Vallesian and Turolian. This pattern in temporal crown cervid distribution does not support a sister group relationship between Muntiacini and Cervini constituting the Cervinae nor an origin of crown Cervidae in the early late Miocene as communicated in recent studies on molecular phylogeny (Gilbert et al. 2006; Hassanin et al. 2012). In contrast, it points to a sister group relationship of Muntiacinae with Cervinae and Capreolinae (which is in accordance with the study on molecular phylogeny by Marcot 2007 and morphological phylogeny by Azanza 1993 and Azanza and Montoya 1995) and an origin of crown Cervidae within the middle Miocene.

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Appendix

Table 1 Early Turolian cervids recorded in European localities

Country:		Spain			France	Germany	Austria	Hungary	Ukraine	
Location:		Puente Minero	Piera	Crevillente 2	Aubignas I	Dorn-Dürkheim 1	Kohfidisch	Csákvár	Novoelisavetovka	Novoukrainka
Reference:		Azanza (2000)	Azanza and Montoya (1995)	Azanza and Montoya (1995)	Azanza et al. (1993)	Franzen and Storch (1975); Franzen (1981)	Vislobokova (2007)	Kretzoi (1951)	Alexeev 1915; Petronio et al. 2007	Korotkevich 1965, 1970
Medium sized	Subfamily incertae sedis									
	Lucentia pierensis	aff.	X							
	Lucentia iberica			X						
	gen. and sp. indet.				X					
	Cervavitus sp.						X			
	Cervavitus variabilis								X	
	Turiacemas concudensis					X	aff.			
	Capreolinae									
	Procapreolus sp.							X		
	Procapreolus loczyi						aff.			
	Procapreolus ucrainicus									X
Small–medium sized	Muntiacinae									
	Amphiprox anocerus					?				
	Muntiacinae gen. and sp. indet.			X						
	Euprox sp.						X	X		
Very small sized	Subfamily incertae sedis									
	Cervavitulus mimus		X		X	X		X		

Table 2 Antler measurements of the studied specimens collected at Dorn-Dürkheim 1

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
Large appendages																
1973		18.04														
1667		17.97	17.02													
1646		17.16	17.50													
1649				17.2	17.75											
3977		19.02	19.47													
1660	41.07	15.62	16.06	16.44	14.39											
1657				17.42	16.49											
1674				14.44	13.32											
1708		17.77														
1701				16.83	16.05											
1707		16.01	16.71	16.06	15.73											
1700		20.75	22.09													
1609		16.66	20.33													
1696	22.80	18.00	21.27	19.42	19.26											
1676	31.32	18.2	16.09	15.56	16.39											
1989				17.01	15.87											
1648				20.58	19.9											
1669	29.98	17.16	18.61	18.13	17.71											
1677				19.49	18.13											
1693	34.34	18.8	18.55	17.92	17.78											
1693		16.05	16.28													
1665	35.95	17.86	15.27													
1674	28.40	17.28	20.79	18.17	19.83											
1685	37.07	17.56	20.66	18.75	20.58											
1692		21.3	21.25													
1682		18.61	21.63													
1688		16.38	19.05													
1702		20.93														
1684	40.35	15.35	16.47	16.60	14.96											
1683				20.91	18.46											
1683				21.60	21.18											
1695		18.08	19.12													
1691	30.16	17.27	19.23	18.80	18.70											
1662		20.49	19.41													

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
1671	36.24	16.14	17.38	16.54	16.96											
1671	28.24	18.31	18.38		16.73											
1670	36.49	16.75	18.84	16.73	17.16											
1680	39.03	18.63	19.72	18.53	17.65											
1665		19.27	19.81													
1665							13.44	12.58								
1663	27.00	19.52	21.05	20.61	19.97											
1668		16.03	19.53													
1653		17.13														
1651	48.31	17.37	18.52	18.00	18.06											
1652							17.08	20.95								
1654				19.46	18.25											
4358	39.82	18.01	18.39	17.66	17.25											
1658	34.00	17.27	16.42	16.59	16.10											
1659	31.13	16.34	18.00	17.26	17.42											
1659	31.92	15.82	17.02	18.35	16.26											
1656		17.66	19.45													
1655				16.91	16.48											
1647				16.44	16.27											
1681	35.57	16.74	18.21	16.11	17.10											
1673	41.01	16.74	17.50	16.31	16.51											
1672	29.13	19.46	19.01	17.17	17.62											
1644	31.59	18.95	21.15	19.45	21.77											
1644	39.00	16.11	17.96	15.85	15.88											
1643	32.12	15.72	17.48	17.13	17.23											
1643	26.86	15.15	16.14	17.22	16.28											
1643	47.19	16.88	17.53	18.56	17.19											
1642				20.46	19.48											
1640	32.75	16.50	16.32	16.85	16.53											
1641				16.18	14.95											
1641				16.29	17.40											
4888		18.89	20.77													
4870		20.09	21.26													
4609	41.52	15.61	15.28	15.81	15.75											
4922	37.55	15.56	15.77	17.42												

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
4895		16.49	16.73													
4895				15.87	15.29											
4864		20.42	22.69													
4988	36.03	19.58	20.17	21.81	20.19											
4981		19.70	23.99													
5007		18.25	18.37													
5000			15.41													
4990	35.99	16.12	16.99		15.92											
4813	28.50	19.08	17.29	18.11	18.59											
4572				16.54	15.01											
4575	35.00	19.19	21.12	19.76	20.45											
wn		14.43	15.45													
4593		14.38	15.62													
4611	33.55	16.84	19.38	17.74	17.70											
4602	28.73	19.00	19.74	19.16	18.10											
4602				17.34	18.07			17.85								
5005	20.00	17.78	21.65	19.77	20.13											
3799	27.70	18.91	17.62	19.20												
5396							11.67	12.39								
4839	24.53	19.82	22.58	21.10	20.98											
4580		18.96	18.55													
4866	29.89	19.79	21.65	20.08												
4357	43.69	15.4	13.90	17.43	15.33											
4852													16.46			
4835		19.50														
4695	34.41	17.08	19.72	15.67	17.73											
4837		16.32	15.98													
1857	26.57	19.66	19.67	20.76	19.60											
1465															12.62	14.77
1957									20.91	16.56		15.73	16.71		12.64	10.50
1754						19.78	25.04									
1554									15.66	14.85			14.40			6.12
1454												16.29	17.24			
2176						34.95	13.11	13.00								
1568									25.05	15.95						

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
2200	35.70	17.77	18.05	17.30	17.56		20.42	22.13								
2186							20.86	19.60								
wn	28.00	20.79	24.33	21.47												
2139							23.8	24.23								
2194							23.88	26.88								
2191		22.29		22.76	20.93											
2188												21.22	17.21			
2182				17.96	17.29											
2168							24.16	21.67								
1537									18.41	18.84						11.38
2164								23.62								
2146						71.84	22.16		23.60	25.26			24.33			16.42
2161							24.60	22.58								
5395							22.78	26.47								
4964	38.51	19.12	22.28	19.16	20.71											
4955				17.92	17.48											
4950	37.04	18.18	18.70	20.95	20.96											
4493				18.13	19.04											
5774	36.51	19.11	21.54	20.63	21.30	114.90	20.64	23.87	23.44	17.48		13.09	16.75			
1722							23.75	22.68								
1723							24.22									
1724								22.98								
1726							24.44	23.99								
1727							19.86	23.43								
1734							17.37	20.42								
1747	24.3	19.94	15.76	16.91	19.55											
1731							18.17	20.40								
1738							22.41	22.81								
1739							15.11	16.89								
1737							18.64	19.79								
1742							19.73	20.58								
1743							17.72	18.86								
1748							19.48	20.84								
1745							17.33	14.59								
1748							21.90									

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
1769							22.31	25.43								
1768							19.35	20.64								
1749							18.39	21.61								
1756							20.38	23.18								
1762							18.88									
1764							18.87									
1765							21.87	23.52								
1766							18.19	22.57								
1794							20.48	21.70								
1736							14.31	17.12								
1773								18.82								
1780								27.45								
1779							18.86	24.61								
1778							17.67	19.27								
1777								26.00								
1776							24.48	25.27								
1775								21.55								
1729							19.89	20.28								
1712							18.77	19.25								
1772							19.94	21.05								
2159							23.58	21.23								
1774							20.49	26.31								
1769							20.05	23.32								
1771							21.14	25.04								
1753							19.33	22.46								
1717							18.66	20.79								
1752								22.97								
1714							22.82	25.41								
1750							23.80	24.04								
1757									20.32	21.88						
1718							23.01									
1720							21.24	23.17								
1730							19.77	23.34								
1710							25.43	27.45								
1715							20.64	18.71								

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
2190							20.97	25.15								
2136						57.00	22.54	22.85	22.67	18.67						
wn							23.65	20.38								
1761							16.71	20.65								
1711							25.81	26.63								
1716							15.48	18.98								
1709							17.61	18.85								
1709							16.09	16.89								
4930						73.93	20.41	22.17	21.24	17.37					12.44	10.66
4829							20.83	20.98								
4880							20.75	21.37								
2187							18.64	20.97								
2183							19.60	22.52								
4980							21.24	23.55								
4994							20.22									
4994							17.30	18.17								
4598							20.21	21.58								
1615							21.20	19.81								
4573							22.74	22.79								
4866							19.83	18.73								
4603				15.91	16.15		13.96	21.26								
4604							20.35	22.66								
4963	22.82	18.84	20.82	20.22	20.80		19.77	23.6								
4962				18.75	19.27		19.96	23.53	22.90	20.91						
4934							19.41	20.55								
4943							23.46	25.42								
4936							16.74	20.24								
4939							15.62	16.04								
4942							13.55	14.86								
4960				15.40	18.29		18.67	21.47								
4965	34.56	18.00	22.57	19.15	20.03		19.82	20.78								
2149							24.42	24.21								
4954				14.79	15.52		16.54	18.07								
4158												16.81	14.81			
4483							13.65	16.75								

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
4539							20.35	21.98								
4940				17.38	17.61		19.50	22.70								
4825						83.00	19.61	22.50	19.59	19.08		14.21	19.42			
4577	41.05	20.43	21.59	21.89	21.4											
4596							17.39	22.11								
4596							20.62	23.42								
4596							21.23	25.76								
2185						64.25	24.46	29.32	24.80	23.31		19.13	22.45		10.42	15.35
2185									20.78	15.43		15.10	14.02			
4809	44.00	15.18	15.37	15.62	14.57		18.08	17.92								
4957				20.04	21.21		24.36	25.87								
4819							21.76	21.28	29.23	16.7		18.55	16.19			
4853							19.56	21.01								
4853						89.00	23.65		24.52	18.64		18.26	16.97			
4853						76.64	21.69	23.54	23.86	20.86						
4522						77.31	18.35	19.25	17.40			15.13	16.18			
4570						87.00	19.23	22.50	28.28	19.62						
4570															12.75	10.20
4903						61.20	21.38	23.09	23.01	18.81		19.87	20.18			
4477							21.19	18.51								
4572						54.86	19.52	20.44	22.62	15.54		15.55	13.94		16.10	12.86
4572							19.02	19.36								
4572							23.24	26.44								
4605	23.18	17.52	20.18	19.28	19.31		21.48	21.87								
4575							19.27	23.42	19.97	17.62						
4575							18.52	18.94								
4826							19.84	22.14								
4859							22.07	23.07								10.35
4910							19.62	21.60	21.51	16.87						
4928							17.12	21.01								
4928							20.18	21.08								
4609							19.40	21.02								
4906							19.22	17.61								
4845							17.74	26.23								
4845							22.74	24.29								

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
4836							15.63	17.04								
4836							24.25	23.72								
4925							19.86	18.96								
4850							15.90	15.61								
4876							12.08	15.85								
4593							20.00	21.31								
4587							16.04	18.35								
2132						93.00									17.02	12.49
2140						100.00	19.83	23.08	21.92	17.25		15.68	15.52			
2138						71.15	17.34	20.86	19.24	16.53		14.42	14.04		14.04	9.37
2157							17.06	19.55	18.30	19.66			15.60			
2137							18.67	17.92	18.92	13.58						
2151							21.51	23.75	20.86	21.08		19.89				
2131									29.09	24.92						
2130						90.00	16.80	20.91	27.42	15.57						
2162						70.79	23.81	24.26	31.91	19.28			17.59			
4360									21.90	14.78		15.26	14.86		11.92	10.02
4604									31.65	19.92		19.35	20.14			15.90
4931						34.66	24.96	22.03				17.57	21.02		13.87	13.04
4606									22.10	15.97						11.94
4606							20.42	18.48								
4933									30.29	19.18		17.57	17.65		14.92	15.50
4597									19.99	16.54			15.68			
4597									17.84	12.92					10.41	7.61
4875												12.05	13.44			
4984									16.50	11.45			10.40			6.32
5015									26.74	16.23		18.89	15.31			9.91
5015									21.43							
4824				18.41	16.41	59.01	20.55	22.86	30.77	18.07			18.78		13.99	13.47
4560									20.06							
4569									16.09	12.79		13.03	12.57	7.23	9.44	5.20
4883						67.74		27.55	28.98	23.47					15.33	11.56
4856												14.58	14.27			10.36
4603									24.4	17.19			17.14			11.27
4573									22.93	20.71					12.19	9.64

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
4819									23.23	66.67						
4807									18.00	16.33			15.21			11.10
4847									27.32	15.19		13.72	14.22			10.27
4847									25.41	16.2						12.38
4863									29.73	19.05						15.08
4863									18.95	14.90						
4863									19.91							
4174									23.67	20.30						
2152						67.24	19.96	20.05	26.31	17.74			17.25			
4586						81.00	19.56	21.32	23.21	18.67						13.25
2158							22.16	20.37	26.74	17.99			18.66			12.52
2153						66.00	19.76	20.35	26.36	14.43			14.39			10.03
2141						52.00	21.8	23.46	20.05							
2174						53.36	22.99	24.32	31.10	20.89		18.79	23.78			11.91
2203						87.35		22.88	22.85	17.22		17.59	16.4			
2203									21.68	18.73			16.98		16.16	12.33
wn									17.61	15.75			12.03			
2203									13.12	12.9		12.85	13.12			7.29
4446									19.24	14.88			15.02			7.62
4336												16.04	20.38			
4156							17.90	15.88								
4470									23.40	19.54						
4519									25.53	19.84		18.96	21.24			14.12
2195						90.77		28.23	28.41	20.59						
4818						84.72	19.20	20.57	26.41	15.05			14.98		11.84	9.18
2168									24.55	19.3					15.21	11.14
2168									28.43	13.84			13.33			
4810						114.13	19.97	22.53	19.22	13.9		14.38	14.56			9.51
2184	27.00	24.00	20.20	21.36	25.07	110.00	24.95	27.29		23.59						
2896						89.25	21.81	24.82	19.05	20.77		17.91	19.40	46.93	14.42	12.94
4808	15.45	21.38	22.55	21.86	21.43		23.40	25.41								
4812									21.98	12.08		12.45	11.54		8.15	5.81
1770							20.94	18.18								
4811							13.89	13.51								
1675	44.46	13.16	14.21	14.98	12.48											

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
1650	36.37	19.82	21.29	19.87	20.9											
4813						23.02	21.27	19.49					16.46	10.71	9.16	6.55
4999								19.45								
5026								14.77								
4991							20.37	19.80								
4843							23.20	23.67								
5003				20.47	21.55		21.54	20.72								
4568							21.67	23.05								
4859							21.23									
4610							14.49	19.31								
4610							15.35	13.15								
5028							19.70	22.27								
5028							15.74	14.19								
2150							21.05	22.51								
2156							23.66	21.30								
2143							22.35	25.76								
2144								22.35								
2135							25.52	23.81								
2197	30.06	19.56	20.50	20.10	20.24		23.21	22.63								
2160							18.43	18.19								
2145							19.75	20.06								
2147							18.00	19.41								
2155							20.44	25.92								
2129							25.25	30.53								
2133							18.97	21.86								
2142							18.73	21.19								
5031						70.35	21.05	20.41	24.98	15.09		17.03	15.45			12.04
4961				16.69	17.48		19.91	21.73								
4953				15.19	14.96		15.59	16.11								
4224							24.73	21.85								
4224				18.69	16.90											
4898							22.12	26.61								
4898							20.84	23.15								
4707							20.65	20.62								
6029						79.05	20.86	21.65	31.39	16.79				52.00	13.32	13.75

Table 2 (continued)

Collection number	Pedicle					Antler s.s.										
						Bbp						Ibp			tine	
	L	PAD	PTW	DAD	DTW	H	PAD	PTW	DAD	DTW	H	PAD	PTW	L	PAD	PTW
4814									26.70	19.36		18.24	19.12		12.50	13.47
4814							19.75	20.40								
4814												16.65	19.24			
4099	26.30	17.16	19.90	21.97	20.09		23.75	25.15								
4817				15.23	15.17		16.76	16.90								
4941				11.79	17.52		20.30									
4945							17.66	18.90								
4948				17.55	17.36		20.97	18.31								
4949	30.55			19.22	18.57											
4950							19.90	20.61								
4951							20.15	22.52								
4944				15.55	13.81		15.31	15.53								
4845							17.56									
4938				14.08												
4160								18.51								
Small appendages																
519		8.25	7.37	8.93	8.94											
520				11.65	10.25		12.02	10.03								
1876							10.39	9.82								
4816							8.74	9.75								
wn				10.19	8.44		12.13	9.36								
4913	26.15	11.50	11.50	11.60	10.36											
518				9.66	8.70		10.76	9.66								

Abbreviations are defined in section Abbreviations

Table 3 Upper teeth measurements of Dorn-Dürkheim 1 specimens included in this study

Premolars				L	W	Molars				L	Wa	Wp
S	wn	r	P2	6.50	6.01	S	508	l	M1	8.26	10.70	9.68
S	1023	l	P3	8.85		S	911	l	M1	8.07	9.06	8.75
S	1070	r	P3	6.63	7.27	S	3782	r	M1	9.81		10.22
S	506	r	P3	7.50		S	wn	l	M1	8.66	9.77	9.34
S	wn	r	P3	7.32	7.87	S	wn	l	M1	8.95		
S	wn	r	P3	7.74	8.75	S	4100	r	M2	9.17	11.46	10.35
S	955	l	P3	7.23	7.09	S	4729	r	M2	9.69	11.13	9.85
S	484	l	P4	6.26	8.99	S	3796	l	M3			9.16
S	513	r	P4	5.65	7.97	S	3807	l	M3	9.16	10.66	9.44
S	906	r	P4	5.98	8.30	S	4671	r	M3		14.73	
S	950	l	P4	6.26	8.07	L	493	l	M1	11.06	12.56	12.08
S	1032	l	P4	8.03	10.37	L	498	r	M1	11.00	12.97	12.30
S	wn	r	P4	6.40		L	499	l	M1	12.05		12.86
L	1020	l	P2	10.43		L	500	r	M1		13.05	
L	1022	l	P2	10.09	8.61	L	502	r	M1			11.73
L	1025	l	P2	9.85	9.31	L	509	r	M1	11.59	13.20	13.06
L	1030	r	P2	11.97	9.18	L	810	l	M1	11.49	13.41	
L	1033	l	P2	9.65		L	811	l	M1	13.28	14.29	13.44
L	1038	r	P2	10.96	8.85	L	828	r	M1	13.10	13.15	12.51
L	1042	l	P2	10.53	9.45	L	830	l	M1	13.48	13.73	13.10
L	1045	r	P2	10.59	8.45	L	836	l	M1	12.36	13.74	12.93
L	1048	l	P2	11.40	9.87	L	840	r	M1	11.99	13.46	12.38
L	1049	r	P2		9.55	L	842	r	M1		14.02	
L	1069	l	P2	9.15	8.44	L	843	r	M1	12.80	13.88	13.44
L	1080	r	P2		8.60	L	846	l	M1	11.94	13.60	12.96
L	1122	l	P2	9.17	8.57	L	1027	l	M1	11.97		13.33
L	1127	r	P2	10.89	9.69	L	1064		M1	11.91	13.30	13.13
L	1129	l	P2	12.02	9.01	L	wn	r	M1	12.21	12.60	12.17
L	3852	r	P2	12.03	9.43	L	wn	l	M1	12.62	13.83	13.63
L	3870	l	P2	10.28	9.77	L	wn	l	M1	11.60	12.81	12.54
L	3946	l	P2	11.35	9.96	L	wn	l	M1	11.38		12.36
L	4344	l	P2	12.00	9.04	L	wn	r	M1	11.30		11.92
L	wn		P2	10.97	9.35	L	804	l	M2	13.63	15.47	14.78
L	1029	l	P2/P3	11.05	9.90	L	809	l	M2	14.81		14.78
L	1040	r	P2/P3		9.19	L	815	l	M2	14.12	15.13	14.52
L	1047	l	P2/P3	10.76	9.79	L	818	r	M2	14.05	15.60	14.70
L	1074	r	P2/P3	10.24	9.31	L	821	r	M2	13.04	14.69	13.84
L	1075	r	P2/P3	11.54	10.09	L	822	l	M2	13.04		
L	1081	l	P2/P3	11.36	10.60	L	825	l	M2	13.62	14.44	14.19
L	1086	r	P2/P3	10.94	10.00	L	826	l	M2	13.64	14.92	14.12
L	1125	l	P2/P3	11.66	10.36	L	832	r	M2	14.98	15.68	15.22
L	1018	l	P3	8.78	9.69	L	833	l	M2	13.54	14.76	14.17
L	1023	l	P3	10.53	10.51	L	835	l	M2	13.77	15.44	14.33
L	1024	l	P3	10.73	11.42	L	839	r	M2	13.76		14.28
L	1026	l	P3	10.74	9.93	L	841	l	M2	13.74	14.44	13.88
L	1031	l	P3	11.05	10.71	L	847	r	M2	13.97	15.77	15.00
L	1043	r	P3	10.15	10.66	L	912	r	M2	14.15	14.90	14.38
L	1046	r	P3		10.54	L	957	l	M2	10.28	13.29	10.83
L	1051	l	P3	9.88	10.24	L	3828	r	M2	12.97		13.30
L	1057	r	P3	10.39		L	3842	r	M2	14.02	15.84	14.97
L	1058	l	P3	10.43	10.88	L	3854	r	M2	14.24	15.05	14.41
L	1060	r	P3	10.15		L	4089	r	M2	13.71		15.15
L	1061	r	P3	11.27		L	4089	l	M2	14.27	14.95	14.12

Table 3 (continued)

Premolars				L	W	Molars				L	Wa	Wp
L	1073	r	P3		11.71	L	4115	l	M2	13.39	14.44	13.33
L	1078	l	P3	10.10	11.98	L	4305	r	M2	12.61	14.42	14.23
L	1086	l	P3	10.19	10.66	L	4382	l	M2	13.65	14.85	14.40
L	1087	l	P3	10.51	10.83	L	4504	r	M2	14.86	15.17	14.95
L	1128	r	P3	11.17	10.43	L	4626	l	M2			14.96
L	3781	r	P3	10.42	10.50	L	4739	l	M2	13.10	15.18	
L	3942	l	P3	9.18	10.75	L	4793	r	M2	13.65	14.21	
L	4249	l	P3	11.10		L	wn	l	M2	13.13	15.24	13.42
L	4486	r	P3	8.85	9.65	L	wn	r	M2	14.00	15.71	14.76
L	4651	l	P3	9.54	10.11	L	806	r	M3/M1	13.20	14.39	14.11
L	1079	r	P3/P4	9.84	11.23	L	806	r	M3/M1	13.14	14.50	13.16
L	1082	l	P3/P4	9.65	10.78	L	808	l	M3		14.02	
L	1121	r	P3/P4	9.66	10.50	L	812	l	M3	14.35	15.39	14.77
L	3849	l	P3/P4	9.88	11.57	L	814	l	M3	13.05		13.98
L	4625	r	P3/P4	9.36	10.43	L	817	r	M3	13.14		13.35
L	1019	l	P4	9.49	11.07	L	820	r	M3	13.34	15.35	13.78
L	1020	r	P4	8.75	11.58	L	823	l	M3			13.44
L	1026	l	P4	9.62	11.33	L	829	l	M3	13.37	14.24	13.50
L	1027	l	P4	8.60	11.29	L	831	r	M3			13.55
L	1028	l	P4	8.23	10.90	L	844	r	M3	13.85	15.00	13.60
L	1034	r	P4	8.70		L	919	r	M3	9.26	10.22	9.63
L	1035	l	P4	8.85	12.18	L	3845	r	M3	14.44	14.87	14.15
L	1036	l	P4	8.59		L	4056	l	M3	13.72	14.75	14.10
L	1037	r	P4	8.77	11.51	L	4081	l	M3	13.01		12.58
L	1039	r	P4	8.56	10.41	L	4103	l	M3			
L	1044	r	P4	8.90	11.47	L	4394	l	M3	13.82	15.48	14.23
L	1048	r	P4	9.02	11.53	L	4413	r	M3	13.42	14.27	13.80
L	1050	l	P4	8.46	11.67	L	4760	l	M3	14.73	15.15	13.86
L	1054	l	P4	8.90	11.26	L	4793	r	M3	12.54	13.95	13.65
L	1055	r	P4	9.29	11.41	L	wn	l	M3	13.45	14.39	13.47
L	1057	l	P4	9.33	10.90	L	wn	r	M3	12.75	13.26	11.32
L	1062	l	P4	8.85								
L	1063	r	P4	9.97	11.61							
L	1065	l	P4	8.89	11.45							
L	1071	l	P4	8.54								
L	1073	r	P4	8.95								
L	1073	l	P4	8.97								
L	1075	r	P4	9.04	12.05							
L	1076	r	P4	8.49	11.28							
L	1085	l	P4	8.99	11.90							
L	1088	r	P4	9.54	12.38							
L	4073	r	P4	8.72	11.64							
L	4089	l	P4	8.97	11.35							
L	4106	r	P4	8.69	11.46							
L	4407	r	P4	8.67	12.09							
L	4506	l	P4	10.13	12.35							
L	4615	l	P4	10.02	12.77							
L	4691	r	P4	8.69	11.10							
L	4763	l	P4	8.76	11.66							
L	wn		P4	9.33	12.40							

r, right; l, left; S, small; L, large; other abbreviations are defined in section Abbreviations

Table 4 Lower teeth measurements of Dorn-Dürkheim 1 specimens studied.

			p2		p3		p4		m1			m2			m3			
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1236	r		5.29	10.58	6.71	11.00	7.41										
L	1209	r							10.65	8.43		12.10	9.42		17.32		8.70	4.84
L	1196	r										12.62	9.32	8.71	18.24	9.27	8.63	4.77
L	1210	l										13.06	9.03	8.44		9.31	8.29	
L	1195	r										12.81	10.03	9.06	19.05	9.38	8.78	5.64
L	1199	r										12.83	9.39	8.60	18.94	8.80	8.65	4.76
L	1269	l			10.26	6.01												
L	1238	r					11.17	7.18										
L	5393	l	8.91[a]	4.75[a]														
L	1240	l					11.09	6.47										
L	1234	l					10.10	5.56										
L	1233	l					10.72											
L	1232	r				7.32												
L	4055	l					10.82	7.49										
L	4079	r						6.85										
L	4200	r					11.35	8.13										
L	1248	l			10.33	6.63												
L	1242	r					10.86	6.50										
L	1243	l					11.27	7.65										
L	1244	l					11.80	7.50										
L	1245	l			10.47	6.92												
L	1255	r	8.38[a]	4.54[a]														
L	1253	r			9.45*	5.30*												
L	1252	l	8.51[a]	4.19[a]														
L	1260	r			10.71	6.84												
L	1251	r	8.22	4.24														
L	1250	r					11.56	6.60										
L	1235	l					10.67	6.74										
L	4092	l			10.72	6.56												
L	4116	r					10.29	7.42										
L	4047	r					11.17	7.68										
L	1257	r					10.93	6.65										
L	1258	r					11.10	7.35										
L	1259	r			10.37	5.86												
L	1261	r	8.70[a]	3.83[a]														
L	1267	r			10.48	6.08												
L	1266	l			10.95	6.88												

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1265	r			9.67	5.41												
L	1264	l			10.94	6.35												
L	1264	r					10.70	7.30										
L	1263	r					10.34	6.68										
L	1249	l					10.91	7.48										
L	1271	l	7.32[a]	3.92[a]														
L	1271	r			7.90[a]	4.93[a]												
L	1272	r																
L	1273	l			10.33	6.48												
L	1274	l	8.63	4.70	10.98	6.59												
L	1270	r	9.06	5.22														
L	1262	r	8.56	4.33														
L	1278	r	9.04	5.12														
L	1283	l					11.12	6.84										
L	5392	l					10.59	6.67										
L	1279	r			10.11	6.32												
L	1237	r					10.35	6.70										
L	4409	r					10.81	6.70										
L	1286	l					11.54	7.23										
L	1287	l			10.80	6.28												
L	1288	r	9.27	5.58														
L	1288	r					11.50	6.77										
L	1290	l					11.58	7.12										
L	1291	r					11.70	6.69										
L	1299	l					10.58	7.15										
L	1300	r	9.38	5.14														
L	1298	r					11.38	6.82										
L	1298	l			10.24	6.60	10.55	7.42										
L	1295	l			10.63	5.75												
L	1296	l					11.33	7.23										
L	1295	r					11.42	7.86										
L	1294	l					11.26	6.66										
L	1293	r					11.50	7.29										
L	1285	r			10.55	6.38												
L	1302	r			10.81	6.48												
L	1303	r					10.17	6.55										
L	1304	l					12.00	7.98										

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1305	r					10.75	6.63										
L	1306	l	7.97[a]	3.66[a]														
L	1315	l	9.30[a]	4.06[a]														
L	1312	r	8.79	5.39														
L	1321	r	8.54[a]	4.42[a]														
L	1323	l	8.89[a]	4.43[a]														
L	1330	r	8.06[a]	4.01[a]														
L	1331	l	9.08	4.80														
L	1331	l	8.34[a]	4.41[a]														
L	1332	l	8.62	4.89														
L	1313	l			9.92	6.00												
L	1301	l			10.61	6.76												
L	1317	l			10.65	6.35												
L	1318	r			10.41	6.52												
L	1324	l			10.30	6.29												
L	1327	r			10.42	5.88												
L	1329	l			10.63													
L	1307	r					10.61	6.16										
L	1307	r					10.49	6.90										
L	1307	r					11.24	6.80										
L	1308	l					11.42	7.08										
L	1316	r					11.20	7.50										
L	1312	r					11.05	7.80										
L	1312	l					10.84	6.83										
L	1311	l					12.02	6.73										
L	1310	l					10.49	6.67										
L	1309	r					10.43	6.27										
L	1325	r					12.49	7.49										
L	1319	l					10.56	6.29										
L	1320	r						7.68										
L	1326	r						6.71										
L	1327	r					11.69	7.40										
L	1327	l					10.90	6.31										
L	1328	r					10.61	7.64										
L		l	7.44	4.17														
L	4630	l	9.01	5.19														
L	4536	l	6.93*	3.78[a]														

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	4702	l			10.82	6.26												
L		l			10.31	6.34												
L	4718	l			10.90													
L		l			10.11	6.35												
L		l			10.21	6.73												
L		r			10.24	6.13												
L	4454	r																
L	920	l			10.60	6.12												
L	4312	l																
L	4666	r			9.78	5.83												
L	4693	r			10.40													
L	4751	l					11.82	7.33										
L		l					11.15	7.06										
L	4614	r					11.23	6.78										
L		l																
L	4690	l					10.96	6.21										
L	4668	l					11.69	6.99										
L	4623	l					11.89	6.86										
L	4702	r					11.02	6.81										
L		l					10.93	7.53										
L		r					10.80	6.91										
L		r					11.20	7.16										
L		l					11.50	7.83										
L	4455	l					10.60	7.39										
L	1197	r							11.79	8.38	8.77							
L	1200	l							12.85	8.58	8.16							
L	1220	l							11.28	8.46	8.98							
L	1188	r							11.84	7.81								
L	1175	l							11.20	8.75	8.93							
L	1160	r							12.31	8.27	8.13							
L	1161	r							12.53	8.21	8.75							
L	1162	l							12.91	8.82	8.90							
L	1151	l							12.06	8.49	8.73							
L	1138	l							12.44	8.49								
L	1141	r							11.21	8.11	8.90							
L	1146	r							11.39	8.60	8.60							
L	1147	l							12.43	8.07	8.90							

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1156	l							12.00	8.33	8.54							
L	1158	r							11.03	8.14								
L	1167	r							11.33	8.57	8.91							
L	1178	l							12.43	8.80	8.35							
L	1181	l							11.98	8.59	8.36							
L	1193	r							12.39	9.15	8.56							
L	4061	r							11.39	9.03	9.21							
L	3834	l							11.76	7.98	7.44							
L	4054	l							12.00	8.64	8.76							
L	3865	l							12.30	8.34	8.89							
L	4393	l							12.44	9.17	8.56							
L		l							12.25	8.17	8.82							
L	4703	l							11.81		8.72							
L		l							11.78		8.76							
L	4672	l							11.64		8.87							
L	4538	l							11.95	8.35	8.72							
L	3881	r							11.73	8.71	8.45							
L	1211	r											10.51					
L	1198	l										12.56	10.39	9.83				
L	1220	l										12.48	9.17	8.24				
L	1186	l										12.23	9.29	8.61				
L	1187	r										13.2	10.47	9.40				
L	1189	r										12.23	9.46	8.83				
L	1171	r										12.47	9.44	9.10				
L	1173	r										12.74	9.79	9.04				
L	1176	r										12.55	9.74	9.13				
L	1177	r										13.22	9.52	9.23				
L	1164	l										12.73	9.90	9.92				
L	1149	l										13.29	9.83	9.30				
L	1135	l										12.37	9.50	8.62				
L	1136	r										13.28	9.81	9.50				
L	1139	r										12.94	9.88	8.93				
L	1142	l										13.05	9.35	8.90				
L	1143	r										12.93	9.81	9.11				
L	1143	l										11.82	10.07	9.39				
L	1144	l											9.50					
L	1157	l										13.49	9.72	9.06				

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1168	r										11.99	9.76	9.01				
L	1180	r										13.44	9.53	9.59				
L	1194	l										13.14	9.92	10.34				
L	1212	r										12.69	10.22	9.59				
L	1212	l										13.1	10.13	9.41				
L	1227	r										13.37	10.01	10.07				
L	1231	l										12.33	9.56	8.07				
L	1230	r										13.55	9.74	9.70				
L	4340	l										12.82	8.65	8.85				
L	4071	r										13.45	9.73	9.10				
L	4068	r										12.94	9.09	8.44				
L	4117	l										12.08	9.94	8.78				
L	3840	r										12.32	9.61	8.98				
L	4645	r										12.75	9.37	9.29				
L	4728	r										11.95	9.72	9.25				
L	4772	l										13.05	9.50	9.55				
L		r										13.32	9.66	9.37				
L	4468	r										12.35		9.77				
L	4385	l										12.15	9.95	9.48				
L	925	l												9.12				
L	4496	l										13.77	9.92	9.26				
L		r										13.08	9.25	9.00				
L	1213	l													18.64	9.57	8.69	5.64
L	1214	l															8.57	4.47
L	1215	r													18.05	8.93	8.40	4.53
L	1216	r													18.39	9.10	8.60	5.22
L	1217	r													18.37	9.90	8.84	5.16
L	1218	l														9.48	9.42	
L	1219	l													17.90	8.86	8.64	5.18
L	1204	r														9.21	8.45	
L	1206	l														9.16	8.30	
L	1207	l														9.76	8.55	
L	1208	r														9.08	7.90	
L	1197	l													18.33	8.66	8.04	4.56
L	1198	l														9.34	8.27	
L	1202	r														9.22	8.80	
L	1177	l														10.05		

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
L	1159	l														9.51	8.68	
L	1163	l														9.50	8.81	
L	1150	l														9.17	8.72	
L	1154	l														9.02	8.52	
L	1157	r														9.32	8.73	
L	5391	l														10.15	9.24	
L	1191	r														9.07	8.06	
L	1203	l														10.01	9.83	
L	1222	l													18.00	8.90	8.24	4.85
L	1225	r													19.10	9.67	9.20	5.46
L	1224	r													18.12	9.22	8.58	5.20
L	1224	r														8.71	8.21	
L	3921	l														10.15	9.04	
L	1376	l														9.52	8.57	
L		l													18.39			5.83
L		r														8.91	8.20	
L		l														8.88	8.23	
L		l														9.31	9.63	
L	4684	l													19.29	9.49		
L	4794	l													16.91	9.19	8.47	4.41
L	4749	r													18.57	8.67	8.13	5.22
L		r														9.31	9.30	
L	4687	r														8.72	8.48	
L	4755	l														9.68	9.07	
L	4494	l														9.13	8.65	
L	4307	r													17.16	8.8	8.54	4.97
L	4528	l													16.59	9.38	8.75	5.53
L	3913	l													17.72	9.73	8.20	5.43
L	4041	r													18.78	9.43	8.88	5.49
L	3873	l													18.27		10.04	5.50
L		r													18.80	9.70		4.83
S	512	l	7.19	3.69														
S	486	l		3.89														
S	514	r	7.57	4.51														
S	954	r			7.89	4.20												
S	951	r			7.64													
S	907	r																

Table 4 (continued)

			p2		p3		p4			m1			m2			m3		
			L	W	L	W	L	W	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	Wt
S	477	l				4.93												
S	514	l				5.08												
S	492	l				4.41												
S	4042	r					8.32	5.65										
S	1289	r						5.65										
S	1276	r					9.40	5.56										
S	4708	r					8.16	5.23										
S	3816	l					8.65											
S	3808	r					8.34	6.40										
S	495	r					8.47	4.73										
S	490	r					8.09	4.88										
S	4708	r					8.42	4.90										
S		r					8.23	5.05										
S	1229	r							11.31	7.64	8.39							
S	1132	r							10.31	6.94	7.07							
S	9786	r							9.56	6.46	6.37							
S	517	r								6.68								
S	942	l							9.73	6.82	6.32							
S	3909	l										10.00	7.05	6.46				
S	547	r										9.62	7.28	7.24				
S	546	r										9.03	6.81					
S	489	l													13.49	6.03	6.11	3.91
S	496	l															6.22	4.43
S	483	l															6.33	3.59
S	504	l															6.32	3.79
S	494	l																
S	4512	l													13.08	6.33	6.04	
S		r															7.48	4.24
S	4674	l														6.41	6.21	
S	943	l														6.24	6.80	

S, small; L, large; other abbreviations are defined in section Abbreviations

[a] Decidual tooth

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