Deer from the Pliocene site of Bad Deutsch-Altenburg 26 (Lower Austria, Leithagebirge): Conclusions based on skeletal morphology

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(With 20 figures and 2 tables)

Abstract

Nineteen skeletal elements from the Pliocene site of Bad Deutsch-Altenburg 26 (Lower Austria, Leithagebirge) could clearly be assigned to cervids. They are distinguishable based on body size and bone characters. *Eucladoceros* sp., *Praeelaphus perrieri*, and *Dama pardinensis* were identified. A pedicle with a fragment of the burr as well as a 2nd anterior phalanx is consistent with *Eucladoceros* sp. and *Arvernoceros ardei*. Two mandibles and a fragmentary metatarsal bone belong to *Procapreolus* sp. or *Croizetoceros ramosus*.

The features of the teeth and skeletal elements of these deer are predominantly plesiomorphic and their development stage corresponds with the cervids from Perrier-Etouaires at about 2.78 myr (NOMADE *et al.* 2014), MNQ16b (GUÉRIN 2007). All recorded deer species are also known from Vialette (MNQ16a), France, considered to be about 3.1/3.2 myr in age (HEINTZ 1970; LACOMBAT *et al.* 2008). This identification is in accordance with the small mammal faunal list (RABEDER 1997). The occurrence of thermophilic taxa such as an early member of the *Dama*-lineage and *Procapreolus* agrees with the presence of *Miniopterus* and *Coluber* and indicates warm climate.

Arvernoceros ardei and *Praeelaphus perrieri* could previously not be separated based on post-cranial skeletal features. Some distinguishing criteria are discussed here. A close relationship between *Arvernoceros* and *Eucladoceros* is discussed on the basis of numerous corresponding skeletal features. The close relationship of *"Cervus" pardinensis*, *"Cervus" rhenanus*, and *Dama nestii* with Middle Pleistocene and recent *Dama dama* (PFEIFFER 1999a, 2005) is further supported and they are therefore combined here in the genus *Dama*. Additional arguments are discussed here with regard to resolving the unsatisfactory priority problem of *Metacervocerus* and *Pseudodama*.

Keywords: Pliocene, Austria, cervids, *Arvernoceros*, *Dama pardinensis*, *Eucladoceros*, *Procapreolus*, *Praeelaphus perrieri*, skeletal characteristics, taxonomy

Kurzfassung

Aus dem Fundhorizont der pliozänen Fundstelle Bad Deutsch-Altenburg 26 (Niederösterreich, Leithagebirge) konnten 19 Skelettelemente eindeutig Cerviden zugeordnet werden. Mindestens

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vier Cervidenarten lassen sich unterscheiden, die in der Körpergröße und an den Knochenmerkmalen deutlich differenziert sind.

Eucladoceros sp., *Praeelaphus perrieri* und *Dama pardinensis* sind eindeutig nachgewiesen. Sowohl zu *Eucladoceros* sp., *Praeelaphus perrieri* als auch zu *Arvernoceros ardei* kann ein Rosenstockfragment mit Geweihansatz passen, zu *Eucladoceros* sp., oder *Arvernoceros ardei* eine 2. Phalanx anterior.

Zu *Procapreolus* sp. oder *Croizetoceros ramosus* gehören zwei Mandibulaäste und ein Metatarsusfragment.

Die Merkmalsausprägungen der Zähne und Skelettelemente der Cerviden von Deutsch-Altenburg zeigen eine Häufung plesiomorpher Charaktere und eine hohe Übereinstimmung in der Entwicklungsstufe mit den Cerviden aus Perrier-Etouaires (2,78 Mio. J. vor heute; NOMADE *et al.* 2014), MNQ16b (GUÉRIN 2007). Alle vorkommenden Cerviden sind aber bereits seit dem unteren Villafranchium (MNQ 16a, vor 3,1/3,2 Mio. Jahren) in Frankreich (Vialette, HEINTZ 1970; LACOMBAT *et al.* 2008) und Italien (Triversa, ABBAZZI *et al.* 1995, *Procapreolus cusanus*) nachgewiesen. Diese zeitliche Einordnung entspricht der nach den Kleinsäugern getroffenen Einstufung von Deutsch-Altenburg 26 (RABEDER 1997). Das Vorkommen warmzeitlich angepasster Hirsche wie *Dama pardinensis*, einem Vorfahren des rezenten europäischen Damhirsches *Dama dama*, und *Procapreolus* sp. steht im Einklang mit dem Nachweis von *Miniopterus* und *Coluber* und spricht für warmes Klima.

Arvernoceros ardei und *Praeelaphus perrieri* sind bisher nicht eindeutig am postcranialen Skelett unterschieden worden. Einige Unterscheidungskriterien werden hier diskutiert. Eine enge Verwandtschaft von *Arvernoceros* und *Eucladoceros* wird wegen der hohen Übereinstimmung der Skelettmerkmale diskutiert. Die enge Verwandtschaft von *"Cervus" pardinensis*, *"Cervus" rhenanus*, *Dama nestii* mit mittelpleistozänen bis rezenten Damhirschen (PFEIFFER 1999a, 2005) wird anhand von weiteren Argumenten bestärkt, sie sind deshalb unter einer Gattung *Dama* vereinigt. Das unbefriedigende Prioritätsproblem mit den Gattungsnamen *Metacervocerus* und *Pseudodama* kann so gelöst werden.

Schlüsselwörter: Pliozän, Österreich, Cerviden, *Procapreolus*, *Dama pardinensis*, *Praeelaphus perrieri*, *Eucladoceros*, *Arvernoceros*, Skelettmerkmale, Taxonomie.

Introduction

The extremely rich vertebrate site of Deutsch-Altenburg (Austria, Leithagebirge) in the Pfaffenberg, the western foothill of the Hainburger Berge, was already mentioned by FREUDENBERG (1914) and later by K. MAIS and G. RABEDER in numerous publications (Fig. 1). Since 1908, Mesozoic dolomites have been mined in several layers in the Hollitzer quarry. Numerous crevices and caves were exposed during blastings.

All the fossil sites in the large Hollitzer quarry, which were discovered and excavated from 1908 to 1984, were designated as Deutsch-Altenburg. They are identified with the numbers 1 to 52 referring to the chronological order of their discovery (FRANK & RABEDER 1997). The site Deutsch-Altenburg 26 is a column filled with large and small vertebrates, which was dated as Middle Pliocene based on small mammals, especially the *Mimomys* species (*Mimomys postsilasensis*, *M. stehlini*). The occurrence of thermophilic

Fig. 1. Location of the site Deutsch-Altenburg in Lower Austria, Leithagebirge.

taxa such as *Miniopterus* and *Coluber* indicates relatively high temperatures (FRANK & RABEDER 1997). In the filling, two fossil layers could be discriminated. The higher-lying layer 26 A (light sand) contained only white bone fragments, whereas the main fauna comes from a reddish-brown clay (fossil layer 26 B) with black bones. These two layers were separated by sterile, stratified sands with hardened parts and dolomite rubble. On top of the succession, modern humus is present (RABEDER 1997). All skeletal elements are very bright, have a firm consistency with an even, non-eroded surface, and show clear bite marks from a powerful carnivore. A possible candidate, *Pachycrocuta perrieri*, is present in the fauna.

Deer have been primarily classified based on their often very impressive antlers, skull characters and teeth. Features of the post-cranial skeleton were mostly neglected. Articulated skeletons with complete antlers are rarely preserved. This also applies to Deutsch-Altenburg 26, where most bone remains are very fragmentary. Under these conditions the unequivocal determination of skeletal elements is particularly important.

Previous studies (PFEIFFER 1998b, 1999a, 2002, 2005) show that the postcranial skeletal features are suitable to determine relationship-lines of deer through the Plio- Pleistocene. Antler characteristics change relatively rapidly. They are the most important features of living deer, used to distinguish individuals from each other and to show physical strength against a rival. Antler strength and morphology change significantly with increasing individual age, which is important for female deer to estimate the fitness of a potential sexual partner, but a challenge for research and resulting taxonomic conclusions if only fragments are preserved. The problem is reflected by numerous taxonomic complications in deer classification. Against this background the determination of post-cranial skeletal characters can provide valuable assistance.

Material and methods

The present skeletal elements of deer from Deutsch-Altenburg 26 are kept at the Institute of Paleontology, University of Vienna (IPUW). The designation DA 26/1 was preliminarily applied to deer bones in the size of recent red deer, DA 26/2 to bones in the size of fallow deer, and DA 26/3 to bone fragments in the size of today's roe deer. Later, the

catalogue numbers were completed, IPUW 7512 prefixed before DA 26/… and consecutive numbers used for the skeletal elements.

The bones from Deutsch-Altenburg 26 were measured following the method of VON DEN DRIESCH (1976). Dimensions and skeletal characters are compared with recent and fossil deer originating from the following sites and collections:

Latest Pliocene and Early Pleistocene

Kaltensundheim, Germany: IQW

Les Etouaires, St. Vallier, France: FSL

Perrier, France: MNHN

Senèze, France: NMB, FSL

Tegelen, the Netherlands: RMNH

Untermaßfeld, Germany: IQW

Valdarno, Tasso F.U., Italy: IGF, Accademia Valdarnese del Poggio Montevarchi

Middle Pleistocene

Clacton, Swanscombe, Jaywick, Great Britain: BMNH

Mosbach, Germany: MNHM

Voigtstedt, Süßenborn, Germany: IQW

Late Pleistocene

Kebara, Israel: Institute for Zoology and Paleontology, Hebrew University, Jerusalem

Neumark-Nord, Germany: LDA

Schlutup, Germany: MNU

Upper Rhine Valley, Germany: HLMD, MNHM, NMS, SMF, SMNK, and private collection Frank MENGER (Darmstadt)

Recent deer skeletons

IHK: *Dama dama*, *Cervus elaphus*, *Cervus nippon*, *Axis axis*, *Capreolus capreolus*, *Alces alces*, *Rangifer tarandus*, *Odocoileus virginianus*

MNHB: *Dama dama*, *Dama mesopotamica*, *Capreolus capreolus*

MTD: *Dama mesopotamica*, *Cervus nippon*

Private collection Christian Oswald (Englmeng, Bavaria): Different subspecies of recent *Cervus elaphus*

SMF: *Dama mesopotamica*, *Cervus nippon*

ZFMK: *Dama dama*, *Cervus elaphus*, *Cervus nippon*, *Axis axis*, *Capreolus capreolus*, *Alces alces*, *Rangifer tarandus*

The remains of a relatively large cervid, recorded under IPUW 7512 DA 26/1, were compared with the taxa *Eucladoceros ctenoides* (NESTI, 1841) from Senèze and Tegelen, *Eucladoceros dicranios* (NESTI, 1841) from the Tasso F.U., as well as *Praeelaphus perrieri* (CROIZET & JOBERT, 1828) and *Arvernoceros ardei* (CROIZET & JOBERT, 1828) from Perrier.

IPUW 7512 DA 26/2 (finds in the size of fallow deer) are compared with *Dama pardinensis* (CROIZET & JOBERT, 1828) from Perrier – Les Etouaires, *Dama rhenena* (DUBOIS, 1904) from Senèze, St. Vallier and Tegelen, and *Dama nestii* AZZAROLI, 1947 from the Valdarno (Tasso F.U.) of Italy. In addition, skeletal morphology is compared with the Middle- and Late Pleistocene fallow deer *D. dama clactoniana* (FALCONER, 1868), *Dama dama geiselana* PFEIFFER, 1998 and extant fallow deer.

IPUW 7512 DA 26/3 (finds in the size of roe deer) are compared with the material of *Procapreolus cusanus* (CROIZET & JOBERT, 1828) from Perrier-Les Etouaires, *Croizetoceros ramosus* (CROIZET & JOBERT, 1828) from Etouaires, Pardines and St. Vallier, and the Middle Pleistocene roe deer *Capreolus suessenbornensis* from the Middle Pleistocene sites Voigtstedt, Süßenborn, and Mosbach in Germany. Fig. 2 gives an overview of the localities compared to Deutsch-Altenburg 26, and the occurring species of deer. It is based on the integrated stratigraphical and biochronological scheme for Late Pliocene – Pleistocene large mammal faunal units (Italy) and biozones (France) published in NOMADE *et al.* (2014).

The compared skeletal material is listed in Table 1. Dimensions published by HEINTZ (1970) are also added.

Abbreviations

BD – distal breadth

BP – proximal breadth

DA – Deutsch Altenburg

GL – greatest length

KD – minimum diameter of the diaphysis

MC – metacarpus

MT – metatarsus

TD – distal depth

TP – proximal depth

Table 1. List of skeletal elements compared to the cervid material from Deutsch-Altenburg 26 broken down by stratigraphic age, locality, taxon and skeletal element.

Skeletal material compared to Deutsch-Altenburg 26							
	skeletal element		Humerus	Radius	MC III+IV	Tibia	MT III+IV
	Locality	**Taxon**	n	n	n	n	n
Latest Pliocene – Early Pleistocene	Perrier	*Praeelaphus perrieri*	17	10	21	15	9
	Perrier	*Arvernoceros ardei*				3	8
	Kaltensundheim	*Arvernoceros* sp.	2	6	3	1	2
	Senèze	*Eucladoceros ctenoides*	12	13	14	10	10
	Tegelen	*Eucladoceros ctenoides*	7	3	2	5	7
	Tasso	*E. ctenoides / E. dicranios*	6	11	14	7	15
	Senèze	*Dama rhenana*	28	29	47	32	40
	St. Vallier	*Dama rhenana*	7	3	14	9	15
	Tegelen	*Dama rhenana*	7	8	7	6	6
	St. Vallier	*Croizetoceros ramosus*	3	3	9	4	13
	Valdarno	*Dama nestii*	20	24	26	20	23
Middle- and Late Pleistocene	Mosbach,Voigtstedt, Süßenborn	*C. elaphus acoronatus*	12	8	14	30	24
	Neumark-Nord	*C. elaphus*	13	14	7	15	10
	Upper Rhine Valley, div. German localities	*C. elaphus*	11	21	16	7	9
	Clacton	*D. dama clactoniana*	1	7	9	11	9
	Jaywick	*D. dama clactoniana*	0	0	2	5	0
	Swanscombe	*D. dama clactoniana*	9	7	9	16	10
	Neumark-Nord	*D. dama geiselana*	58	56	53	64	59
	Upper Rhine Valley, div. German localities	*Dama dama*	5	7	10	5	7
	Kebara	*Dama mesopotamica*	20	6	6	21	7
	Süßenborn, Mosbach,	*Praemegaceros verticornis*	1	1	5	1	2
	Bilshausen	*Praemegaceros verticornis*	2	2	1	2	2
	Upper Rhine Valley, div. German localities	*Megaloceros giganteus*	14	41	40	45	44
	Mosbach	*Capreolus suessenbornensis*	17	15	8	27	17
	Suessenborn, Voigtstedt	*Capreolus suessenbornensis*	0	1	0	2	0
recent	German collections	*Cervus elaphus*	41	41	22	41	29
		Cervus nippon	28	28	32	28	34
		Dama dama	46	44	58	52	52
		Dama mesopotamica	26	41	17	28	35
		Axis axis	14	15	12	14	12
		Capreolus capreolus	25	23	42	53	25

Fig. 2. Integrated stratigraphic and biochronological scheme for Late Pliocene – Pleistocene large mammal faunal units (Italy), biozones (France) and German Pleistocene localities compared with Deutsch-Altenburg 26 and the occurring species of deer based on NOMADE et al. (2014).

Ma	MNQ		Polarity	Localities	Avernoceros ardei	Avernoceros sp.	Praeelaphus perrieri	Eucladoceros sp.	Eucladoceros ctenoides	Eucladoceros dicranios	Eucladoceros giulii	Dama pardinensis	Dama lyra (Italy)	Dama rhenana	Dama nestii	Dama farnetensis	Dama nestii vallonetensis	Dama roberti	Dama sp.	D. dama clactoniana	D. dama geiselana	Croizetoceros ramosus	Procapreolus cusanus	Capreolus cusanoides	Capreolus suessenbornensis
0.12	MNQ 25	Eem	BRUNHES	Neumark-Nord																	●				
	MNQ 22 (Middle Pleistocene)		BRUNHES	Clacton, Swanscombe																●					
				Pakefield, Solilhac															●						
				Mosbach														●							○
				Süßenborn														●							○
0.78				Voigtstedt														●							○
1.0	MNQ 20	Epivillafr.	Jaramillo	Untermaßfeld		?					●							●					○		
1.5	MNQ 19	Late Villafr.	MATUYAMA	Farneta					●						●	●									
1.7				Tasso F.U.		?		●	●	●					●										
	MNQ18			Senèze					●						●										
1.8				Tegelen					●						●										
			Olduvai																						
	MNQ 17a	Middle Villafr.		St. Vallier				●						●	●							●	?		
				Pardines				●						●											
2.78	MNQ 16b	Early Villafranchian		Montopoli F.U.											●										
				Perrier-Etouaires	●	○		●						●								●		○	
				Deutsch-Altenburg	?	?	○	●						●								?	?		
3.15 3.60	MNQ 16a			Vialette	●	○		●						●								●	○		

Institutional abbreviations

BMNH – British Museum of Natural History, London

FSL – Faculté des Sciences de Lyon

IGF – Museo di Storia Naturale dell'Università di Firenze

IHK – Institut für Haustierkunde der Christian-Albrechts-Universität, Kiel

IQW – Institut für Quartärpaläontologie, Weimar

HLMD – Hessisches Landesmuseum, Darmstadt

LDA – Landesamt für Denkmalpflege und Archäologie, Sachsen-Anhalt, Landesmuseum für Vorgeschichte, Halle

MNHB – Museum für Naturkunde der Humboldt-Universität Berlin

MNHM – Naturhistorisches Museum, Mainz

MNHN – Institut de Paléontologie du Muséum national d'Histoire national, Paris

MNU – Museum für Natur und Umwelt, Lübeck

MTD – Museum für Tierkunde, Dresden

NMB – Naturhistorisches Museum, Basel

NMS – Naturkundemuseum Stuttgart

RMNH – Nationaal Natuurhistorisch Museum, Leiden

SMF – Senckenbergmuseum, Frankfurt

SMNK – Staatliches Museum für Naturkunde, Karlsruhe

ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn

Identification of skeletal elements

Based on 100 articulated skeletons and partial skeletons of Late Pleistocene *D. dama geiselana* and *C. elaphus* from Neumark-Nord (Saxony-Anhalt, Germany), the morphology of the fallow deer and the red deer was studied intensively. Ontogenetic stages, sexual dimorphism, variation of bone and tooth features, the antler development in all ontogenetic stages, as well as the variation range of the dimensions and proportions are investigated in PFEIFFER (1998a, 1999b). Neumark-Nord can serve as a reference for many other sites when it comes to estimating the variation within a cervid species. Based on this dataset, PFEIFFER (1999a) developed a distinguishing catalogue for fossil and recent plesiometacarpal deer including antler- and tooth characters and especially postcranial skeletal characters.

Increasingly more Pleistocene deer species were later included (PFEIFFER 2002, 2005). This made it possible to identify plesiomorphic characters and to detect homoplasy in several cases. Consequently, each cervid species shows a mixture of plesiomorphic and apomorphic character states. PFEIFFER (1999a) provides a skeletal analysis and distinction catalogue for the following taxa: *Eucladoceros ctenoides*, *E. dicranios*, *Dama rhenana*, *D. nestii*, *D. d. clactoniana*, *D. d. geiselana*, *D. dama*, *D. mesopotamica*, *Cervus elaphus*, *C. nippon*, *Axis axis*. The distinguishing characters are discussed and figured and their distribution in the studied material is given in tables.

The quality of the distinguishing features is very different. Often they cannot be identified clearly in young animals, are less developed in females, or polymorphism exists. Functional adaptations can be detected in the occipital region of the skull, the breadth of cervical vertebrae, the distal length of their alae, and the proximal part of the humerus with increasing antler development. For phylogenetic conclusions these issues need to be considered. Accordingly, PFEIFFER (1999a) excluded several discussed skeletal features for the phylogeny reconstruction of fossil and recent plesiometacarpal deer. In the following years, telemetacarpal deer were also included in the data base: *Capreolus capreolus*, *C. pygargus*, *C. suessenbornensis*, *Rangifer tarandus*, *Alces alces*, *Cervalces latifrons*, and the plesiometacarpal *C. elaphus acoronatus*, *Megaloceros giganteus*, and *Praemegaceros verticornis* (PFEIFFER 2002, 2005). In these papers the description of the skeletal characters and their character states are listed in a table in English. The distinctive catalogue is applied here to the Pliocene cervids of Deutsch-Altenburg 26.

Currently the data base has been enlarged with the taxa *Arvernoceros ardei* and *Praeelaphus perrieri* from Perrier. The results of the skeletal analysis will soon be presented in a separate paper.

The skeletal characters and their different character states are pictured in PFEIFFER 1999a. These illustrations can be used for comparison with the deer from Deutsch-Altenburg 26. Very often the plesiomorphic character states pictured for *Eucladoceros ctenoides* (= *E. tegulensis* DUBOIS 1904a) or *Dama rhenana* occur in the cervids from Deutsch-Altenburg 26 (see discussion below).

Taxonomic considerations

Class Mammalia LINNAEUS, 1758

Order Artiodactyla OWEN, 1848

Family Cervidae GOLDFUSS, 1820

Subfamily Cervinae GOLDFUSS, 1820

Genus *Arvernoceros* HEINTZ, 1970

Arvernoceros ardei (CROIZET & JOBERT, 1828)

Cervus ardei was described by CROIZET & JOBERT, 1828 from Early Villafranchian deposits of Perrier (MNQ 16), a cervid in the size of modern red deer. HEINTZ (1970) proposed the genus *Arvernoceros* with the type-species *Arvernoceros ardei* (CROIZET & JOBERT, 1828) from Perrier, separating this species based on differing skeletal morphology from *Cervus* s. str.

The antler construction is simple, the pedicle is relatively long, and the first basal tine is situated high above the burr; slightly flattened, projecting prongs may occur in the basal region. The beam is long, circular in cross section at the base, may be flattened above the first anterior tine (Kaltensundheim), and ends in a small terminal palmation in adult specimens. The postcranial elements are hardly distinguishable from *Praeelaphus perrieri*. *P. perrieri* seems to be slightly smaller in body size but with overlapping size ranges with *Arvernoceros ardei* in bone dimensions (DEPERET 1884). A few characters on the postcranial bones can be used to separate these species (see discussion below).

Genus *Eucladoceros* FALCONER, 1868

The first occurrence of *Eucladoceros* FALCONER, 1868 in France was predated to the Early Villafranchian (MNQ 16a) recently (VALLI *et al.* 2005). Teeth from Vialette could be assigned to *Eucladoceros*. They are significantly bigger than teeth of *Praeelaphus perrieri*, and they are morphologically distinct from *Arvernoceros*. *Eucladoceros*, studied

in a comprehensive analysis by HEINTZ (1970), is abundant in the Middle Villafranchian (Pardines, St. Vallier and others), and is well known from the Early Pleistocene of France (Senèze), the Netherlands (Tegelen), and Italy (Valdarno). *Eucladoceros ctenoides* (NESTI, 1841) (= *Cervus tegulensis* DUBOIS, 1904a; = *Cervus teguliensis* DUBOIS, 1904b; = *Cervus senezensis* DEPERET & MAYET, 1910) has impressive comb-like antlers with numerous long and flattened, forward-directed tines. The antler morphology is more complicated in the type species of *Eucladoceros dicranios* [= *Cervus* (*Eucladoceros*) *sedgwickii* FAL-CONER, 1868] from the Upper Valdarno. The comb-like structure is preserved at the base but the long forward-directed tines show several bifurcations resembling the branches of a tree. The morphology is comprehensively pictured in AZZAROLI & MAZZA (1992). The body size of *Eucladoceros* strongly increased from the late Pliocene to the late Early Pleistocene. *Eucladoceros giulii* KAHLKE (1997, 2001) was described from Untermaßfeld in Germany (Jaramillo Event), significantly exceeding *E. ctenoides* and *E. dicranios* in body size. In CROITOR (2005, 2014) this species is referred to *Arvernoceros*. The postcranial skeleton of *Eucladoceros* species can be morphologically distinguished from Pleistocene cervids of comparable size range such as *Cervus elaphus*, *Praemegaceros*, and *Megaloceros* but show high conformity with *Arvernoceros ardei* (see discussion below).

Genus *Praeelaphus* PORTIS, 1920

Praeelaphus perrieri (CROIZET & JOBERT 1828)

The subgenus *Cervus* (*Praeelaphus*) was proposed by PORTIS (1920:133) for the Early Villafranchian species *Cervus arvernensis* CROIZET & JOBERT, 1828, *Cervus perrieri* CROIZET & JOBERT, 1828 and *Cervus etueriarum* CROIZET & JOBERT, 1828, but no type has been designated. Noticing the significant morphological differences with respect to *Cervus elaphus*, HEINTZ (1970) assigned *Cervus perrieri* to *Cervus* sensu lato, so its systematic position remained open. CROITOR (2012) has chosen *Cervus perrieri* as type of the genus *Praeelaphus*. GRUBB (2000) discussed that *Cervus perrieri* may be identical with *Cervus pardinenis*. This is not the case: *Praeelaphus perrieri* is clearly distinguishable from *Cervus pardinensis* CROIZET & JOBERT, 1828, the type species of *Metacervocerus* DIETRICH, 1938. Therefore, following CROITOR (2014), it can be excluded that *Praeelaphus* is a synonym of *Metacervocerus* as mentioned by GRUBB (2000).

Genus *Dama* FRISCH, 1775

Cervus pardinensis CROIZET & JOBERT, 1828 was described from the Late Pliocene localities of Etouaires and Pardines, and *Cervus philisi* SCHAUB, 1941 was described from the Early Pleistocene localities Senèze, St. Vallier, and Chilhac. The latter species is identical to *Cervus rhenanus* DUBOIS, 1904a, b from Tegelen. Also represented by rich bone material are the findings representing *Dama nestii* AZZAROLI, 1947 from the stratigraphically

younger Valdarno. In 1992, AZZAROLI established the genus *Pseudodama* including the species *Dama nestii* (type species) with the subspecies *"Pseudodama" nestii nestii* and *"P." nestii eurygonos*, and the species *"P." pardinensis, "P." rhenana, "P." lyra, "P." farnetensis, and "P." perolensis*. The latter is an imperfectly known species from Peyrolle, possibly identical to *"P." nestii* (AZZAROLI 1992). Unfortunately *"Pseudodama" pardinensis* is the type species of the genus *Metacervocerus* DIETRICH, 1938. Moreover, also *Cervus philisi* (= *Cervus rhenanus*) in original spelling was included in the genus *Metacervocerus*. Therefore the genus *Pseudodama* is partially preoccupied by *Metacervocerus* (GRUBB 2000).

PFEIFFER (1998a, 1999a and 2005) demonstrated in detailed studies the close relationship of these early medium-sized deer with the extant fallow deer. Trying to resolve the taxonomical implications, PFEIFFER (2005) pointed out that the antler morphology of *"P." lyra* also fits with the description given by FRISCH (1775) for the genus *Dama*. Also *"P." nestii* and *"P." farnetensis* show flattened terminal antler tines in several specimens. All included species belong to the *Dama*-lineage, and the morphological characters are in concordance with a gradual evolution from the Pliocene to the recent species. Accordingly, *Pseudodama* is considered as a younger synonym of *Dama*. Already HEINTZ (1970) focused on the gradual evolution from *Cervus pardinensis* originating from Etouaires to *Cervus philisi* (= *Dama rhenana*) from St. Vallier and Senèze.

The taxa from St. Vallier, Senèze, Tegelen, and the Upper Valdarno are therefore listed under the generic name *Dama* (FRISCH 1775), compared here with IPUW 7512 DA 26/2.

In PFEIFFER (1999a, 2005), *Dama* seemed to form a monophyletic group since the Late Pliocene, leading to the recent fallow deer *Dama dama* and *Dama mesopotamica*. The actual relationship seems to be more complex. *Pseudodama lyra* (AZZAROLI, 1992) from Italy was excluded in the skeletal analysis by PFEIFFER (1999a) because of the insufficient number of postcranial bones. In her cladistic analysis, only species with extensive postcranial skeletal material could be considered. Contrary to the view of CROITOR (2006), *Dama rhenana* and *Dama nestii* are proved to be ancestors of the more modern *Dama*-members (BT 100% for *Dama rhenana*, and 91% for *Dama nestii* in PFEIFFER 2005) based on extensive skeletal material. The relationship of other described Latest Pliocene and Early Pleistocene *Dama*- members is less certain, based solely on the antler and skull characteristics. *Dama nestii eurygonos* is treated as a separate species (*Dama eurygonos*) by several authors (BREDA & LISTER 2013; CROITOR 2014) but is assigned to the genus *Axis* by PETRONIO *et al.* (2013). Within the postcranial bone material of *Dama nestii*, PFEIFFER (1999a) identified only a few medium-sized deer bones that may belong to a second species, differing in morphology and with a slightly bigger size (compare figs 109, 113, 114 in PFEIFFER 1999a). Therefore the numerous postcranial elements do probably belong to the numerous preserved skulls and antlers of *D. nestii*, whereas little material of *D. nestii eurygonos* (original spelling by AZZAROLI) is preserved. The assignment of the postcranial bones in CROITOR (2006: figs 10, 11) to *"Dama" eurygonos* and *"Cervus" nestii* conflicts with the distinction characters of SCHMID (1965), BOSOLD (1968), LISTER (1996), and PFEIFFER (1999a). Metacarpus IGF 394 and metatarsus IGF

399 assigned to *"Cervus" nestii* fit well with *Dama*-characters of SCHMID (1965: figs 57, 58), LISTER (1996: fig. 2 part 6, 10) and PFEIFFER (1999a: fig. 64, character 6; fig. 79, character 2, 3, 6). In the pictured radius IGF 394 assigned to *"Cervus" nestii* (CROITOR 2006: fig. 10C), the margo lateralis forms a distant lip as pictured for *Dama rhenana* (Se 1096) and *D. dama geiselana* (NN 17) in PFEIFFER (1999a). The juvenile specimen IGF 397 assigned to *"Dama" eurygonos* (fig. 10 A, B in CROITOR 2006) is more difficult to assess but is in accordance with the character states given by SCHMID, LISTER, and PFEIFFER for *Cervus elaphus*.

The stratigraphically younger *Dama nestii vallonetensis* was recently upgraded to species level (CROITOR 2014). This has further complicated the *Dama*-relationship line. In the *Dama*-antlers of Pakefield and Soleilhac named *Dama roberti* by BREDA & LISTER (2013), the second anterior tine is absent. This may be a shared derived feature between late *Pseudodama farnetensis* (original spelling of AZZAROLI 1992), *Dama nestii vallonetensis*, and *D. roberti*, indicating close relationship, although a derivation from the primitively three-point *Dama rhenana* was not excluded by BREDA & LISTER (2013). In this case, *D. roberti* would be the sister group of the stratigraphically younger *Dama dama* members derived from *Dama nestii*. They all share a second anterior tine about 20 cm above the burr. BREDA & LISTER (2013) agree with PFEIFFER (2005) in the species included in the *"Pseudodama"*- *Dama*-lineage, but neglect the taxonomic problem with the preoccupation by *Metacervocerus*.

CROITOR (2014) assigned the deer of the *Dama*-lineage to different genera based on skull- and antler characteristics. The change from elongated antler beams to wide laterally orientated antlers indicates many functional adjustments to the occipital and the cervical vertebrae (LENGSFELD 1975; PFEIFFER 1999 a, b). The length and direction of the pedicles and the expression of the crista nucha need to change with antler position. The construction of very large, complex antlers therefore leads to a variety of adjustments to the skull itself. Reinforcements of the skullcap and the occipital region are necessary if broad, heavy antlers are formed, *e.g.*, in *Praemegaceros* and *Megaloceros*. Relatively to its body size, *Dama dama* has the heaviest antlers of modern deer (LENGSFELD 1975). This context must be considered in assessing taxonomic decisions. Several of these functional adaptations can be tracked in the *Dama*-lineage. The shortening and differing direction of the pedicles, as well as the change of an elongated braincase to a shorter more upright-orientated braincase in adult male deer with a strong nuchal crest, reflect a strong muscle insertion area to handle increasingly heavy antlers. Azzaroli (1947) was the first to picture the gradual change of the occipital region. In the female skulls an ontogenetically influenced change of the skullcap is evident. Up to the age of four years the skullcap is clearly domed, reminiscent of the Kindchenschema in *Axis axis* (n=18) and *Dama dama* (n=24). With increase in individual age the braincase elongates and flattens in both species.

A well-known skull character of *Dama dama* is the elongated nasal bones reaching, or overlapping, the frontline of the orbita in lateral view. This feature is shared by the Early Pleistocene *Dama rhenana* from Senèze, the Middle Pleistocene *Dama clactoniana* –

visible in the famous skull from Swanscombe (BMNH 16349), *e.g.*, displayed in SICKEN-BERG (1965) – and the recent *Dama dama* and *Dama mesopotamica*. In addition to the postcranial and tooth characteristics this makes a strong argument for the relationship within this lineage.

Subfamily Capreolinae BROOKES, 1828

Genus *Procapreolus* SCHLOSSER, 1924

The genus *Procapreolus* was established by SCHLOSSER (1924). VALLI (2010) recently presented a comprehensive overview of the distribution of the genus *Procapreolus* and the relationships between *Procapreolus cusanus* and the living roe deer (*Capreolus*).

Procapreolus cusanus reaches the antler development stage of Pleistocene roe deer, although the characteristic pearl structure on the surface of recent *Capreolus* antlers is missing. Teeth and bone dimensions fit the Middle Pleistocene roe deer *Capreolus suessenbornensis* from Mosbach. In this species a pearl structure on the surface of the antlers is developed, weaker expressed than in the recent roe deer.

Genus *Croizetoceros* HEINTZ, 1970

Croizetoceros ramosus (CROIZET & JOBERT, 1828)

The antler development of *Croizetoceros ramosus* is quite different from *Procapreolus cusanus*. *C. ramosus* shows complex antler morphology with numerous, forward-orientated, flattened tines.

Between *Procapreolus cusanus* and *Croizetoceros ramosus* from Etouaires, Pardines, and St. Vallier, a high level of conformity in dental and skeletal characteristics is evident. A distinction based on bone dimensions is difficult (HEINTZ 1970).

Our own observations show several similarities among both *Procapreolus cusanus* and *Croizetoceros ramosus* with extant telemetarpal deer (see discussion below). The conformity is high with *Capreolus* in the dental features and certain morphological characteristics of the postcranial skeleton (PFEIFFER 2000). Therefore *Croizetoceros ramosus* is classified in this study in the Capreolinae.

Description and taxonomic identification of the skeletal elements

Skull

Eucladoceros sp. vel. *Arvernoceros ardei* vel. *Praeelaphus perrieri*

M a t e r i a l : Gnawed fragment of pedicle with burr- and beam-fragment (IPUW 7512 DA 26/1/1, erroneously labeled as DA 26/2)
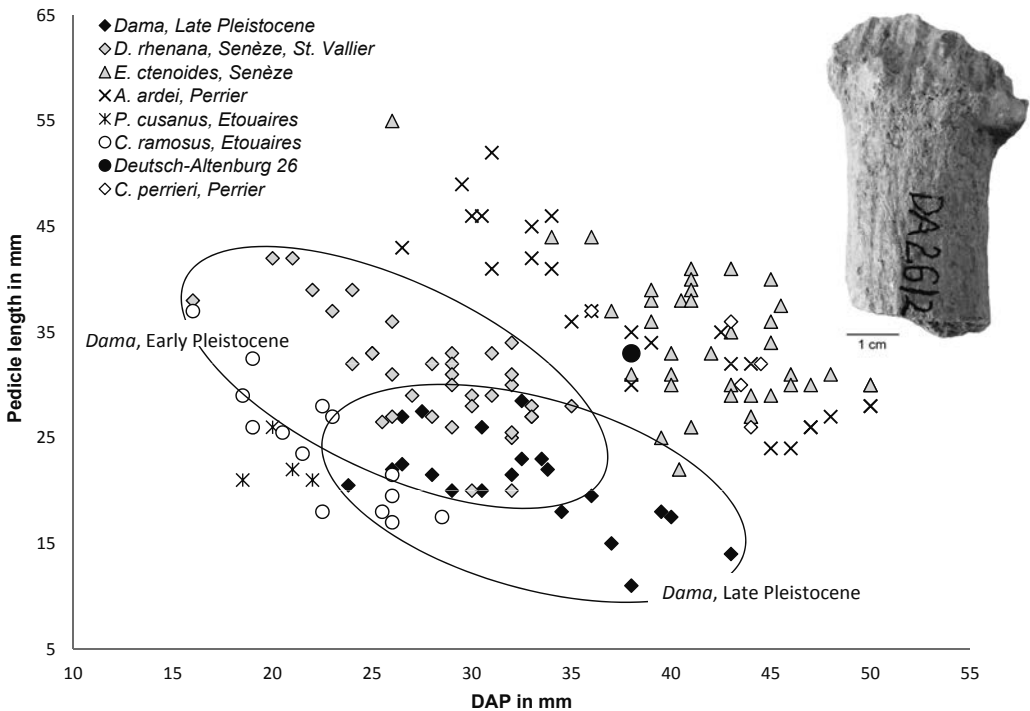
Fig. 3. The long pedicle IPUW 7512 DA 26/1/1 was initially designated to DA 26/2 (cervid in *Dama*-size). The width-length ratio of the pedicle, however, does not fit with a cervid in the size of *Dama*. *Eucladoceros* sp., *Praeelaphus perrieri* and *Arvernoceros ardei* are potential candidates.

D e s c r i p t i o n : Up to the broken edge, the pedicle has a height of 38 mm. It is not widened in the area of the broken edge, which would indicate the transition to the skull, so it must have been actually longer in the living deer. The cross-section is slightly oval and has a diameter of 33 mm and 30.2 mm. At both levels a few millimeters may be missing by gnawing of a carnivore. The antler base has a riffled surface.

Pedicle diameter and length are influenced by ontogenetic growth in cervids. In juvenile deer the pedicle is long and narrow; it then progressively shortens and thickens with antler development and individual age.

In addition to this general effect the pedicles of Pliocene and Lower Pleistocene deer are usually longer than in Middle Pleistocene to Recent deer. In the *Dama*-lineage this phenomenon can be observed from the sites St. Vallier, Senèze, Tegelen, the Upper Valdarno, Swanscombe, Riano, Neumark-Nord, and the Upper Rhine Valley up to recent fallow deer.

Comparing the measured pedicle diameter with dimensions of *Dama rhenana* from Saint Vallier and Senèze, a pedicle diameter of 32 mm fitted to a pedicle height of a minimum of 20 mm and maximum of 34 mm. In Late Pleistocene fallow deer (finds from the Upper Rhine Valley and Neumark-Nord, Lower Saxony), 32 mm pedicle diameter

fitted to a height of a minimum 22 mm to maximum 28 mm (Fig. 3). Therefore the elongated pedicle of IPUW 7512 DA 26/1/1 does not fit into a cervid in the size of *Dama*. HEINTZ (1970) gives comparable dimensions for young males of *P. perrieri*, *Eucladoceros ctenoides*, and *Arvernoceros ardei*. These taxa match the breadth-length ratio of the pedicle from Deutsch-Altenburg 26 (Fig. 3).

Eucladoceros sp. vel. *Arvernoceros ardei*

Material: 2nd anterior phalanx (IPUW 7512 DA 26/1/2).

Description: The bone of the 2nd anterior phalanx has a firm consistency but is strongly gnawed at the surface. In posterior view the distal trochlea forms an elongated peak axially (marked in Fig. 4), a distinctive feature between 2nd phalanges of the front and hind limb (BOSOLD 1968), compare (PFEIFFER 1999a: fig. 81, 5a).

The diaphysis is strong, only somewhat slimmer than the distal trochlea. The proximal attachments of tendons are expressed as bulges; the axial bulge is especially pronounced, thickened in posterior view. The greatest length (GL) is 48.2 mm, the minimal breadth 17.1 mm.

The dimensions of *Eucladoceros* from St. Vallier and Senèze and Pliocene *Arvernoceros* from Kaltensundheim correspond to the dimensions of the 2nd anterior phalanx from Deutsch-Altenburg 26. Morphologically the 2nd anterior phalanges are indistinguishable between these taxa. From Perrier, no comparative data from *Praeelaphus perrieri* and
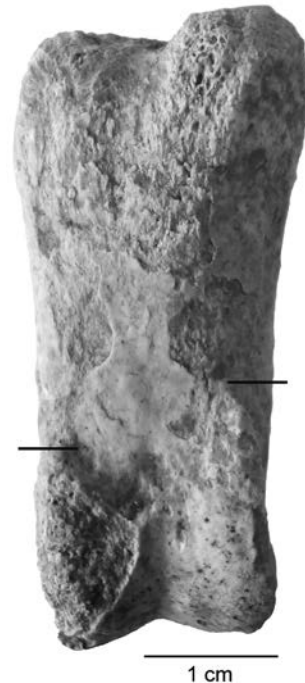
Fig. 4. The 2nd anterior phalanx IPUW 7512 DA 26/1/2 corresponds morphologically and in dimensions with *Eucladoceros* sp. and *Arvernoceros ardei*. In posterior view the distal trochlea forms an elongated peak axially, a distinctive feature between 2nd phalanges of the front and hind limb. The length difference of the axial and lateral trochlea part is marked with black lines.

1 cm

Fig. 5. Right tibia IPUW 7512 DA 26/1/8: Laterally on the cochlea tibiae is the attachment of the tibiofibular cranial ligament, visible as a slight bulge (arrow). This plesiomorphic morphology corresponds with *Eucladoceros* sp. and *Praeelaphus perrieri*.

Arvernoceros ardei are available for the 2nd anterior phalanx. A more detailed taxonomic allocation is not possible.

Eucladoceros sp.

M a t e r i a l : Tibia (IPUW 7512 DA 26/1/8).

D e s c r i p t i o n : The distal end of the right tibia with about 5 cm of the diaphysis is preserved. In the area of the broken edge of the diaphysis, tooth marks of a large carnivore are visible (Fig. 5). The medial malleolus is broken up to the medial articular surface. Of the lateral facies in contact with the os malleolare, the backwards directed portion is broken.

A distal breadth (BD) of 55.2 mm (+ max. 3 mm) could be estimated, the distal depth (TD) is 45.3 mm. The minimum breadth of the diaphysis (KD) is 37.5 mm in the preserved fragment. It is always measured on the tibia in the lower third of the diaphysis, so that the value is likely to come close to the actual value despite the incompleteness of the bone.

The distal breadth of the tibia corresponds to the largest dimensions of Perrier, *Eucladoceros ctenoides* from Senèze, and the lower size range of *Eucladoceros* from the Tasso fauna (Fig. 6). The sexual dimorphism is up to 15 % in bone dimensions of heavy cervids with large antler development. Based on the extensive cervid bone material from Neumark-Nord this could be proven for *D. dama geiselana* and *C. elaphus* (PFEIFFER 1999b). Partial skeletons of *E. ctenoides* have been preserved from Senèze
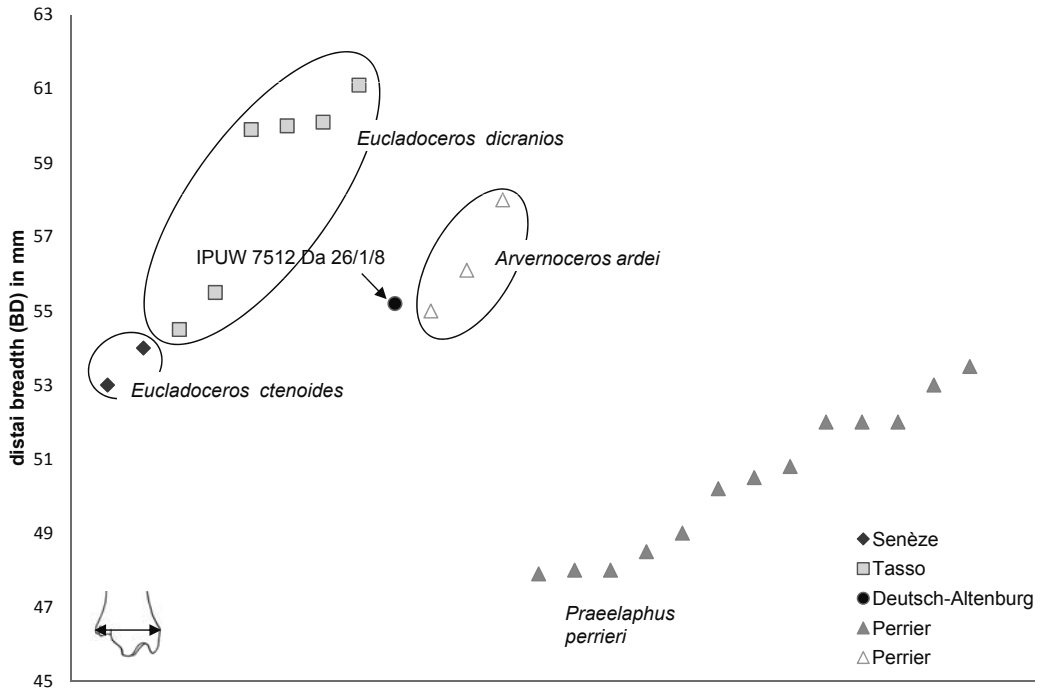
Fig. 6. The distal breadth of the tibia IPUW 7512 DA 26/1/8 is compared with *Eucladoceros* from Senèze and the Upper Valdarno, and with *Praeelaphus perrieri* and *Arvernoceros ardei* from Perrier. The dimensions of IPUW 7512 DA 26/1/8 fit with *Eucladoceros* and *Arvernoceros ardei*. *Arvernoceros ardei* can be excluded based on morphology. *Preaelaphus perrieri* differs in lower dimensions. The tibia fits best with *Eucladoceros* sp.

and also show a significant sexual dimorphism. Therefore the tibia may correspond with females of *E. dicranios* or males of *E. ctenoides*. The three highest values from Perrier belong to *Avernoceros ardei*. The cochlea of the tibia in this species is very plump (see CROIZET & JOBERT 1828: pl. 4, fig. 3 and explanation in the morphological characteristics below) and separates it from the smaller tibiae of *Praeelaphus perrieri* from Perrier.

Morphological characteristics: Only three morphological characters that can be used for taxonomic identification of cervids could be compared due to the conservation status of the distal tibia.

1. In dorsal view the cochlea tibiae forms an asymmetrical tip, laterally pointing. Laterally located on the cochlea tibiae is the attachment of the tibiofibular cranial ligament, visible as a slight bulge in IPUW 7512 DA 26/1/8, *Praeelaphus perrieri* (n=15), *Eucladoceros*, and in several other Pleistocene and Holocene cervid species (marked in Fig. 5). Compare also PFEIFFER (1999a: fig. 74A 7a, 8a). This feature expression may merely be plesiomorphic. The genus *Cervus* s. str. can be clearly distinguished by the lack of the bulge, whereas it is very prominent in the

Dama-lineage. *Arvernoceros ardei* (n=3) differs in this feature from *Praeelaphus perrieri*: it has a very plump cochlea tibiae, and the lateral edge of the cochlea tibiae is convex.

2.   In distal view the posteriorly directed facies in contact with the Os malleolare is small, clearly separated from the plantar directed facet, and the lateral tibial trochlea is only slight reduced in breadth dorsally (PFEIFFER 1999a: fig. 73A). This plesiomorphic feature expression is shared by IPUW 7512 DA 26/1/8, *Praeelaphus perrieri*, *Eucladoceros* and several other modern genera of cervids. From this plesiomorphic character state, several different apomorphic character states evolve in *Cervus* and *Dama* (see discussion in PFEIFFER 1999a).

3.   In axial view the approach of the medial collateral ligament tarsi on the medial malleolus is mostly straight, horizontally clearly separated in IPUW 7512 DA 26/1/8, in *Eucladoceros*, in the *Dama*-lineage but also in *Capreolus* and several other genera (compare fig. 72B in PFEIFFER 1999a). Other genera of deer such as *Cervus* s. str. *Axis*, *Alces*, and *Megaloceros* display a different morphology (PFEIFFER 1999a, 2002, 2005).

R e s u l t s : The verifiable characteristics on the tibia IPUW 7512 DA 26/1/8 show plesiomorphic character states consistent with *Praeelaphus perrieri* and *Eucladoceros*, whereas *Arvernoceros ardei* can be distinguished from these morphologically. The size range of the distal breadth agrees with *A. ardei*, *Eucladoceros ctenoides* from Senèze, and possible female specimens of *Eucladoceros dicranios* (Fig. 6). From *Praeelaphus perrieri* all measured values are below the value of IPUW 7512 DA 26/1/8. The present tibia fits best with *Eucladoceros*.

Humerus

Praeelaphus perrieri

M a t e r i a l : Left humerus (IPUW 7512 DA 26/1/3)

D e s c r i p t i o n : The distal joint is preserved up to the transition to the diaphysis, with distinct bite marks in the transition to the diaphysis. On the lateral epicondyle the outermost edge is broken off. The broken edge is fresh, not dyed. The animal was adult because a growth plate is no longer discernible.

The distal breadth (BD) is about 56 mm (+2 mm max. for minor damage); the maximum diameter of the medial trochlea is 39.5 mm.

Dama pardinensis

M a t e r i a l : Right humerus (IPUW 7512 DA 26/2/4)

The distal joint is preserved up to the approach of the diaphysis. The dorsal medial section next to the olecranon fossa is missing because of strong bites. The animal was adult
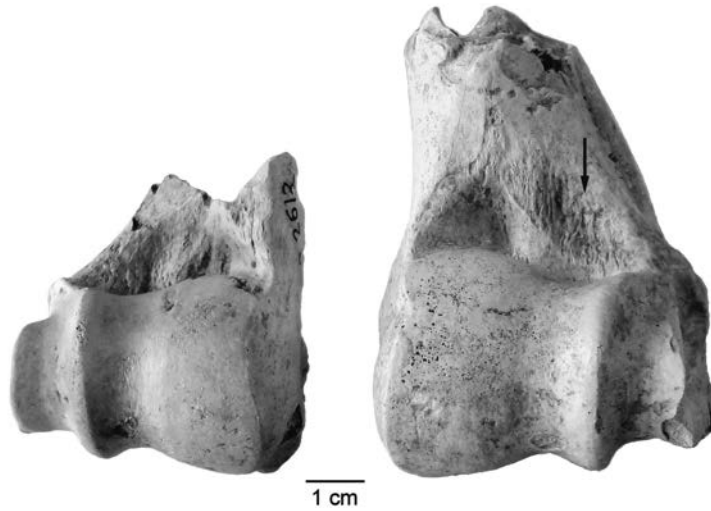
Fig. 7. The trochlea humeri of IPUW 7512 DA 26/2/4 (left) and IPUW 7512 DA 26/1/3 (right) in comparison: The humerus IPUW 7512 DA 26/2/4, with a relatively narrow trochlea in relation to the distal breadth, indicates that this bone belongs to a member of the *Dama*-lineage. The trochlea is axially significantly wider than laterally in IPUW 7512 DA 26/1/7 assigned to *Praeelaphus perrieri*.
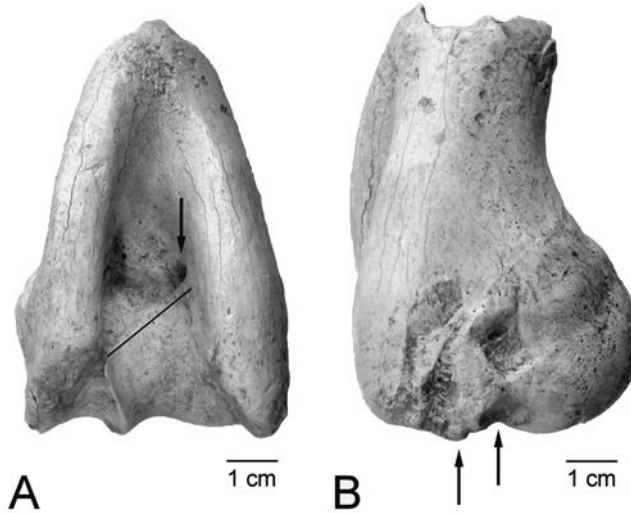

Fig. 8. **A**: Dorsal view: Olecranon fossa of IPUW 7512 DA 26/1/3: From medial to lateral the margin of the trochlea slopes downwards into the olecranon fossa in a diagonal line. The fossa is axially especially deep (arrow). **B**: Medial view: The medial epicondyle of IPUW 7512 DA 26/1/3 is limited only by a straight edge that has a weak cusp (arrow) with a subsequent, significant depression in the center (arrow).

because no growth plate is visible. The distal breadth (BD) is 51.2 mm; the maximum diameter of the trochlea is 34 mm axially.

M o r p h o l o g i c a l   c h a r a c t e r i s t i c s : Six characteristics that affect the distal joint of the humerus are discussed. Characters that are uninformative for the selected species are neglected here. Only four of them could be studied in IPUW 7512 DA 26/2/4. These characteristics are published in PFEIFFER (1999a, 2002, 2005). Table 5 of PFEIFFER (1999a) shows the distribution of features for the taxa *Eucladoceros*, the *Dama*-group, *Cervus elaphus*, *Cervus nippon*, and *Axis axis*.

1.   The trochlea is axially clearly wider than laterally (IPUW 7512 DA 26/1/3, compare PFEIFFER 1999a: fig. 54 B, 4a) or rather slender (IPUW 7512 DA 26/2/4, compare PFEIFFER 1999a: fig. 54 A, 4b).

2.   The fossa radialis has two scores; the lateral one is formed weaker, with a rough surface (IPUW 7512 DA 26/1/3 and IPUW 7512 DA 26/2/4, arrow in Fig. 7).

3.   There is no (PFEIFFER 1999a: fig. 56 B, 6c) or only a weakly developed distally directed bulge on the lateral epicondyle (PFEIFFER 1999a: fig. 56 A, 6b) in IPUW 7512 DA 26/1/3. This assessment is not entirely certain because of slight damage.

4.   From medial to lateral the margin of the trochlea slopes downwards into the olecranon fossa in a diagonal line (IPUW 7512 DA 26/1/3, Fig. 8A, compare also PFEIFFER 1999a: fig. 56 D, 7b). In contrast, the margin is more horizontally directed, often running out laterally in a wavy, blurred boundary (IPUW 7512 DA 26/2/4, compare PFEIFFER 1999a: fig. 56 C, 7a).

5.   In IPUW 7512 DA 26/1/3 the olecranon fossa is particularly deep axially (Fig. 8A, arrow), whereas it is shallower in IPUW 7512 DA 26/2/4.

6.   In medial view the medial epicondyle is limited only by a straight edge that has a weak cusp with a subsequent, significant depression in the center in IPUW 7512 DA 26/1/3 (Fig. 8B).

D i s c u s s i o n : The characters 1, 2, 3 show a probably plesiomorphic character in IPUW 7512 DA 26/1/3.They are less pronounced compared to cervids of comparable body size from the Pleistocene and Holocene. In these probably plesiomorphic features, IPUW 7512 DA 26/1/3 is consistent with *Praeelaphus perrieri*, *Eucladoceros*, and *Arvernoceros ardei* from the Pliocene and Lower Pleistocene. These characteristics may occur even in recent species.

The following distinct feature is assumed to be also plesiomorphic: The margin of the trochlea is expressed as a diagonal line, sloping downwards into the olecranon fossa from axial to lateral (feature 4, compare Fig. 8A). IPUW 7512 DA 26/1/3 shares this character state with *Praeelaphus perrieri*, *Eucladoceros*, *Arvernoceros*, *Praemegaceros*, *Megaloceros*, *Cervus* s. str., and *Alces*, but also with significantly smaller species such as *Rangifer* and *Capreolus*, while the *Dama*-lineage can be distinguished by a more horizontally directed boundary edge, often running out laterally in a wavy, blurred boundary since the Pliocene. The latter expression is also found in the preserved fragment IPUW 7512 DA 26/2/4.
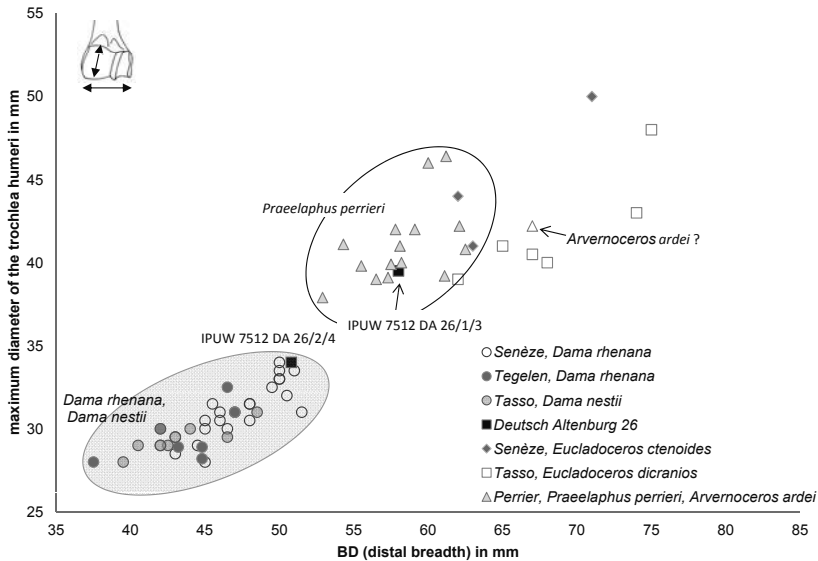
Fig. 9. Distal breadth of the humerus in relation to the maximum diameter of the trochlea humeri: IPUW 7512 DA 26/1/3 fits within the scatter values of *Praeelaphus perrieri*; IPUW 7512 DA 26/2/4 fits within the variation of *Dama rhenana*. The relatively low diameter of the trochlea humeri of *Dama* is clearly visibly in contrast to *Eucladoceros*, *Arvernoceros ardei* and *Praeelaphus perrieri*.
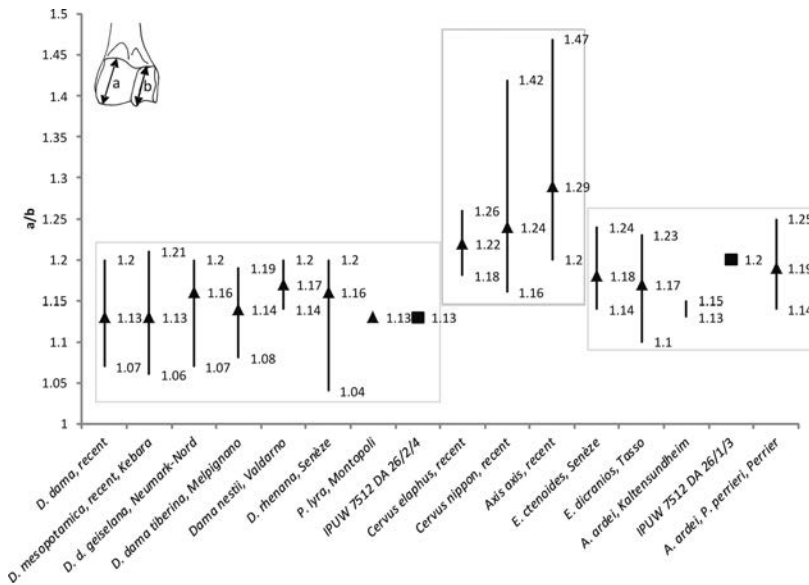

Fig. 10. Proportions of the trochlea humeri: In the *Dama*-lineage it is relatively narrow from the Early Pleistocene until today (grey box). In *Cervus* s. str. and *A. axis* it is medially thick, showing higher variability in *C. nippon* and *A. axis*. *Praeelaphus perrieri* shares the trochlea proportion with *C. elaphus*, while *Eucladoceros* and *A. ardei* come close to the values of *Dama*. The latter can be clearly distinguished by size.

The relatively narrow trochlea humeri in relation to the distal breadth expressed in IPUW 7512 DA 26/2/4 indicates a member of the *Dama*-lineage (Figs 8, 9, 10). Dividing the distal breadth by the maximum diameter of the trochlea yields a value of 1.51 for IPUW 7512 DA 26/2/4. This corresponds exactly to the arithmetic mean of *Dama rhenana* from Senèze and Tegelen (n=29; max. 1.61; min. 1.44), whereas in the Upper Valdarno *Dama nestii* the arithmetic mean of 1.48 (n = 9; max. 1.58; min. 1.40) is slightly lower. The humeri from Perrier, belonging to *Praeelaphus perrieri* and *Arvernoceros ardei* (n=17; max. 1.25; min. 1.14; arithmetic mean 1.43), and *Eucladoceros* from Senèze (n=12; max. 1.54; min. 1.34; arithmetic mean: 1.43), and the Tasso fauna of the Valdarno (n=6; max. 1.47; min. 1.34; arithmetic mean: 1.41) come close to the proportion of IPUW 7512 DA 26/1/3 with the value 1.44.

A particularly deep depression in the olecranon fossa (feature 5) occurs in telemetacarpal Plio–Pleistocene deer up to recent cervids. It is common in *Croizetoceros ramosus* as well as in the genus *Alces*, *Capreolus*, and *Rangifer*. Among the plesiometacarpal deer this expression is occasionally present, whereas it is typical for *Praemegaceros verticornis* and *Megaloceros giganteus* (PFEIFFER 2002, character 24). In IPUW 7512 DA 26/1/3 a deep depression in the olecranon fossa is axially confined to a small spot (Fig. 8A, arrow). This differs from the characteristics observed in the taxa mentioned above. In IPUW 7512 DA 26/2/4 the olecranon fossa is shallower, like in the *Dama*-lineage.

R e s u l t s : Summarizing the present character states, the accordance of IPUW 7512 DA 26/1/3 is greatest with *Praeelaphus perrieri*. The metrical analysis leads to the same result. The sexual dimorphism of the humerus is significant in cervids with strong antlers (PFEIFFER 1999a, b). IPUW 7512 DA 26/1/3 falls below the scatter of the distal breadth values of potential females of *Eucladoceros* from the Early Pleistocene sites Senèze and the Upper Valdarno. The genus *Eucladoceros* may be excluded for the present humerus. This distal humerus IPUW 7512 DA 26/1/3 is therefore assigned to *Praeelaphus perrieri*.

The right distal humerus IPUW 7512 DA 26/2/4 agrees morphologically with the *Dama*-lineage, and the measurements lie in the upper range of *Dama rhenana* from Senèze (Fig. 9). Thus it is highly likely that IPUW 7512 DA 26/2/4 is an early representative of the *Dama*-lineage of the developmental stage *Dama pardinensis/rhenana*.

In IPUW 7512 DA 26/1/3, in medial view the epicondyle is bound by a straight edge that has a weak bulge with a subsequent, significant depression in the center (feature 6, Fig. 8B, arrows). A distinct depression is common in *Eucladoceros ctenoides* (n=17) and *E. dicranios* (n=7). Two specimens of *E. ctenoides* from Senèze (NHMB) had no depression. It is also common in the material from Perrier assigned to *P. perrieri*. One very strong distal humerus possibly belonging to *Arvernoceros ardei* showed no depression.

Fig. 11. Proximal end of the radius of IPUW 7512 DA 26/1/4 with strong bite marks. Based on dimensions it is assigned to *Praeelaphus perrieri*. The insertion area of the lateral collateral ligament at the proximal radius slopes straight downwards (arrow). The medial border forms is only a slight medial bulge rather than a clearly protruding lip.
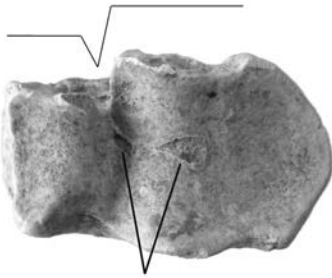

Fig. 12. Top view on the proximal end of the radius IPUW 7512 DA 26/1/4: The recess in the fovea begins with a strong central rounding, becomes narrower, and laterally continues into the fissure capitis radii (arrows). With high probability this is a plesiomorphic character. The margin of the setting surface of the ulna closely resembles that of *Eucladoceros* and *Arvernoceros*.

Radius

Praeelaphus perrieri

Material: right radius (IPUW 7512 DA 26/1/4)

Description: The proximal articular joint with the approach of the diaphysis is preserved (Fig. 11). Strong bite marks are present below the joint. Mirrored, the right radius end fits closely with the left humerus described under IPUW 7512 DA 26/1/3. Both bones could be remnants of a single individual. The proximal breadth (BP) is 56.3 mm, the proximal depth (TP) 32.5 mm.

Morphological characteristics: Four morphological characters can be examined in the present radius fragment; they were used in PFEIFFER (1999a) to distinguish Pleistocene from recent cervids.

1. The insertion area of the lateral collateral ligament at the proximal radius slopes straight downwards (fig. 57B, 1c in PFEIFFER 1999a). This character state is present in IPUW 7512 DA 26/1/4 (Fig. 11, arrow) as well as in *Arvernoceros ardei* of Perrier (PFEIFFER, in preparation). In *Eucladoceros* from different Pleistocene sites and in *Praeelaphus perrieri*, the attachment of the lateral collateral ligament sticks out laterally, forming a small step-shaped shoulder laterally to the diaphysis

below the proximal articular joint (PFEIFFER 1999a: fig. 57A, 1a). However, since the steep ligament insertion area also occurs in stratigraphically younger taxa such as *Alces*, *Megaloceros*, and *Cervus elaphus* (PFEIFFER 2002, 2005), all of which have a considerable body size and carry strong antlers, this feature could be functionally influenced.

2.   The medial border in IPUW 7512 DA 26/1/4 forms no clearly protruding lip; there is only a slight medial bulge (fig. 57B, 3b in PFEIFFER 1999a). This feature expression is also found in *Eucladoceros*, *Arvernoceros*, and *Praeelaphus perrieri*, and is considered plesiomorphic. Based on this undifferentiated expression, more specialized expressions evolve in Pleistocene and extant cervids. On the one hand a significantly protruding lip can be formed on the medial border in the *Dama*-lineage (PFEIFFER 1999a: fig. 57C, 3a), or on the other hand the medial border can be bent flat such as in *Cervus* s. str. (PFEIFFER 1999a: fig. 57B, 3b).

3.   The fovea capitis radii may have differently shaped fossae, which are depicted and investigated in PFEIFFER (1999a). In IPUW 7512 DA 26/1/4 a character expression is present, wherein the recess in the fovea begins with a strong central rounding, becomes narrower and laterally continues into the fissure capitis radii (marked in Fig 12). Compare also fig. 58A, 4a of PFEIFFER (1999a). With high probability this is a plesiomorphic character because it occurs in several Plio-Pleistocene and extant cervids of different body sizes. These include *Eucladoceros*, *Arvernoceros*, *Praeelaphus perrieri*, *Dama rhenana*, and *Axis*. The narrowing may continue to the point where two separate, round fossae arise. This expression occurs with higher frequency along with the plesiomorphic character state in *Eucladoceros* and is common in the genus *Cervus* s. str. in the Pleistocene and Holocene.

4.   Looking at the setting surface of the ulna in view of the fovea capitis radii, the margin is initially flat, rough, forms a clear indentation in the region of the fissure capitis radii and then runs out evenly, creating a clear, step-shaped margin (marked in Fig. 12). This feature expression is found in IPUW 7512 DA 26/1/4 as well as in *Arvernoceros* from Kaltensundheim and in *Eucladoceros*.

R e s u l t : The features studied underline the plesiomorphic character of this radius fragment and do not allow further taxonomic distinction between *Eucladoceros*, *Arvernoceros*, and *Praeelaphus perrieri*. The proximal breadth agrees with the dimensions of *Praeelaphus perrieri* from Perrier, whereas *Eucladoceros* and *Arvernoceros* always surpass this dimension. It is most likely that the radius IPUW 7512 DA 26/1/4 belongs to *Praeelaphus perrieri*.

Metacarpus

Praeelaphus perrieri

M a t e r i a l : right proximal metacarpus III+IV fragment (IPUW 7512 DA 26/1/5), left proximal metacarpus III+IV (IPUW 7512 DA 26/1/6)

Description: Recorded under IPUW 7512 DA 26/1/5, the proximal rest of the MC III is preserved, MC IV is lacking by longitudinal splitting in the area of the sulcus longitudinalis. Dorsally, approximately 4 cm are preserved from the diaphysis, palmar about 5 cm are preserved. The bone shows bite marks on the diaphysis. No meaningful dimensions or morphological criteria could be obtained. Size and proportions of this right MC III fragment may fit to the preserved proximal third of the left MC III+IV.

The left MC III+IV IPUW 7512 DA 26/1/6 shows small bite marks below the proximal epiphysis. Axially, a 5-mm-thick piece of bone is splintered off. The break is dyed , not fresh. The proximal breadth (BP) is 43.9 mm (+ max. 3 mm), the proximal depth (TP) 34.2 mm. These values correspond to the range of variation of *Praeelaphus perrieri/ Arvernoceros ardei* (n=21; BP: max. 45 mm; min. 37.2 mm; arithmetic mean: 41.6 mm) and *Eucladoceros ctenoides* from Senèze (n=5; max. 49 mm; min. 43 mm; arithmetic mean: 43.4 mm). HEINTZ (1970) provides data on *E. ctenoides* from Senèze (n=36; BP max. 50 mm; min. 38 mm; arithmetic mean 44.06 mm).

Based on the size and preservation, the fragmentary metacarpal bones may fit with the preserved humerus and radius listed under IPUW 7512 DA 26/1/3 and IPUW 7512 DA 26/1/4.

Morphological characteristics: Two morphological features were selected and analyzed in the present left metacarpus.

1. In dorsal view the sulcus longitudinalis of MC III+IV can be expressed as a deepened channel (plesiomorphic), a weak fissure, or only a thin, recessed line. In IPUW 7512 DA 26/1/6. only a weak fissure is still preserved (PFEIFFER 1999a: fig. 62, 1a). From Perrier 21 metacarpals are studied. In the four strongest metacarpals the deepened sulcus longitudinalis is visible; all smaller specimens share a sulcus longitudinalis expressed as a small fissure as in IPUW 7512 DA 26/1/6. In *Avernoceros ardei* from Kaltensundheim the plesiomorphic character state is also present. Therefore this may be a distinguishing character between *Praeelaphus perrieri* and *Arvernoceros ardei*. In *Eucladoceros* from Senèze, Tegelen, and the Upper Valdarno the apomorphic expression occurs with low frequency in addition to the plesiomorphic character state (PFEIFFER 1999a, table 9, character 1).

2. In palmar view a significant gap may remain in the region of the fusion of the proximal end of MC III+IV (PFEIFFER 1999a: fig. 63A, 2a, plesiomorphic), or only a narrow channel is visible (PFEIFFER 1999a: fig. 63C, 2b), or MC III+IV are grown together, so that no gap is visible (PFEIFFER 1999a: fig. 63B, 2b). These expressions reflect differing degrees of fusion of MC III+IV. In IPUW 7512 DA 26/1/6 no gap is visible (Fig. 13, arrow). In *Eucladoceros* the plesiomorphic character state occurs together with the apomorphic character state (compare PFEIFFER 1999a, table 9, character 2). In the metacarpals from Perrier (n=21), in the four largest specimens a gap is preserved, whereas in all smaller specimens no gap is visible. Both groups do not overlap in their size range. Therefore the gap may be a distinguishing feature between *Arvernoceros ardei* and *Praeelaphus perrieri*.

Fig. 13. Proximal end of the left MC III+IV of IPUW 7512 DA 26/1/6 in palmar view: MC III+IV are fused, leaving no gap (arrow). IPUW 7512 DA 26/1/6 shares this character state with *Praeelaphus perrier*i, whereas *Arvernoceros* and *Eucladoeros* (most specimen) preserve a gap in this area.

Even in Pleistocene specimens of *Cervus elaphus* the gap is still very common, but is frequently closed in extant red deer. This feature is influenced by ontogenetic growth.

R e s u l t s : In the high degree of intergrowth of MC III+IV the metacarpus IPUW 7512 DA 26/1/6 agrees with the smaller specimens of Perrier, probably belonging to *Praeelaphus perrier*i. In *Eucladoceros* from Senèze, Tegelen and the Upper Valdarno the derived character state occurs rarely beneath the plesiomorphic feature expression. The dimensions of MC III+IV also fit *Praeelaphus perrieri*.

Dama pardinensis

M a t e r i a l : juvenile left metacarpal III+IV (IPUW 7512 DA 26/2/5)

D e s c r i p t i o n : The juvenile age of this MC III+IV is proven by the lack of the distal epiphysis, which is not broken off and was not fused to the diaphysis. The minimum diameter of the diaphysis (19 mm) fits with the size of females and juveniles in Plio-Pleistocene *Dama* (*Dama rhenana*, Senèze juv. KD: 21.5–17 mm; n=6; *D. dama geiselana* ♀ KD: 20–18 mm; n=7; *D. dama geiselana* juv. KD: 20.5–17 mm; n=12).

In dorsal view in the border area of MC III and MC IV only a weak line is visible on the diaphysis; palmar the sulcus longitudinalis is not indented and deeply inclined (see description above). These character states agree with the *Dama*-lineage.
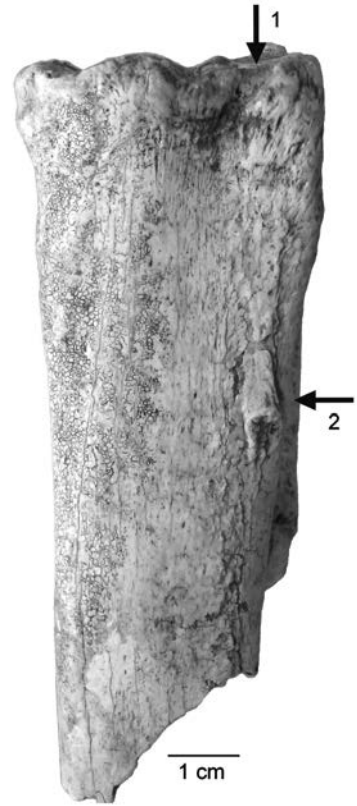
Fig. 14. Proximal end of the right MT III+IV of IPUW 7512 DA 26/1/7 in axial view: A bump on MT III between the dorso–medial and plantar joint surface is weakly developed, followed by a depression (arrow 1). This character expression fits best with *Praeelaphus perrieri*. Significantly raised bumps with a rough bone structure 45 mm distal to the proximal articular surface, possibly indicating intergrowth with a rudimentary MT II (arrow 2).

Fig. 15. Top view on the proximal epiphysis of MT III+IV from IPUW 7512 DA 26/1/7:
The plantar transversally directed facies exceeds the canalis metatarsi proximalis slightly (arrow 1). IPUW 7512 DA 26/1/7 shares this expression with *Praeelaphus perrieri*. Axially between the articular surface of MT III and the facet for the cuneiforme 1, a small bump and a following depression (arrow 2) are visible, contrary to the MT III+IV of IPUW 7512 DA 26/3/4 (Fig. 17).
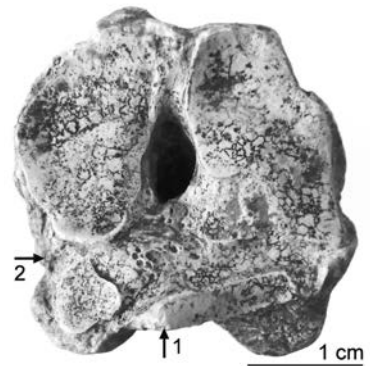
Metatarsus III+IV

Three preserved metatarsal bones IPUW 7512 DA 26/1/7, IPUW 7512 DA 26/2/7 and IPUW 7512 DA 26/3/4, belonging to different deer species, are discussed comparatively. The morphological features provide good evidence for meaningful taxonomic identification.

Praeelaphus perrieri

M a t e r i a l : right proximal metatarsal III+IV (IPUW 7512 DA 26/1/7)

D e s c r i p t i o n : The proximal end of a right MT III+IV is preserved with approximately one-third of the diaphysis. Strong bite marks are present laterally on the broken edge (Figs 14, 15).

Significantly raised bumps, with a rough bone structure, arise 45 mm distal to the proximal articular surface, possibly indicating intergrowth with a rudimentary MT II. A well-developed rudimentary MT II emphasizes the primitive character of IPUW 7512 DA 26/1/7 (Fig. 14).

The proximal breadth (BP) 39.8 mm and depth (TP) 43.2 mm of the metatarsal are within the size range of *Praeelaphus perrieri*. In large cervids the smallest diameter of the diaphysis (KD) is located usually in the upper third of the diaphysis, so that the specified measure of approx. 25 mm (KD), also in this incomplete MT III+IV, should be quite reliable.

Dama pardinensis

M a t e r i a l : fragment of right proximal metatarsal III (IPUW 7512 DA 26/2/6), fragment of left proximal metatarsal III+IV (IPUW 7512 DA 26/2/7)

D e s c r i p t i o n : IPUW 7512 DA 26/2/7 is a fragment of the proximal end of the MT III+IV, which is preserved up to one-third of the diaphysis. The diaphysis is split diagonally. Dimensions cannot be determined, but the estimated size corresponds to the *Dama*-lineage (Fig. 16).

Procapreolus sp. vel. *Croizetoceros ramosus*

M a t e r i a l : fragment of right proximal metatarsal III+IV (IPUW 7512 DA 26/3/4)

D e s c r i p t i o n : The articular surface of the MT III and the dorsal part of the MT IV is preserved. The dorsal part of the diaphysis is preserved up to one-third of its length, while the plantar part is bitten off (Fig. 17). The preserved but incomplete proximal breadth (BP) of IPUW 7512 DA 26/3/4 is 23.1 mm. The estimated size corresponds to the Pliocene *Croizetoceros ramosus* as indicated by the comprehensive measures given by HEINTZ (1970) for the localities St. Vallier (n=19), Villaroya (n=19), and Etouaires (n=14). *Capreolus suessenbornensis* from the Middle Pleistocene German localities Süßenborn (n=1) and Mosbach (n=14) shows the same size range in proximal breadth between BP: max. 24.5 mm, min. 22.5 mm.

M o r p h o l o g i c a l   c h a r a c t e r i s t i c s : The features studied on MT III+IV are partially pictured in PFEIFFER (1999a: fig. 77). Material and character distribution for the *Dama*-lineage and *Eucladoceros* from Senèze, Tegelen, and Tasso F.U. is given in table 12 in that study. In the metatarsals from Perrier (n=17) assigned to *Praeelaphus perrieri*

or *Arvernoceros ardei*, a few morphological differences could be detected that split these metatarsals in two groups and may help in a further distinction between these taxa.

1. In dorsal view the proximal articular surface of MT III is significantly lower than that of the MT IV in IPUW 7512 DA 26/1/7 and IPUW 7512 DA 26/3/4. This character state was also detected in six specimens from Perrier. In *Eucladoceros* the articular surface of MT III and IV project usually on approximately the same level (PFEIFFER 1999a). In the metatarsals from Perrier, three share the character state of *Eucladoceros*. Even in *Croizetoceros ramosus* from St. Vallier (FSL, n=13), this expression was observed. IPUW 7512 DA 26/2/7 cannot be assessed with respect to this feature.

2. In axial view in *Eucladoceros* a bump is strongly developed on MT III between the dorso-medial and plantar articular surface (fig. 77A, 1a in PFEIFFER 1999a). It can be followed by a depression. The bump is absent in the larger species from Perrier (n=6); the metatarsal of this taxon merely has a depression between the medial and plantar articular surface as pictured for *C. elaphus* in PFEIFFER 1999a: fig. 77D, 1c. In the slightly smaller species from Perrier, possibly *P. perrieri* (n=5), the bump is variable in strength; it can be expressed simply as a thickening (PFEIFFER 1999a: fig. 77C, 1b). This character state also occurs in IPUW 7512 DA 26/1/7 (Fig. 15, arrow 2). This feature cannot be assessed definitively because of gnawing marks. In IPUW 7512 DA 26/2/7 the bump seems to be missing, although bite marks complicate the assessment.

    In IPUW 7512 DA 26/3/4 the proximal articular surface of the MT III has a straight, continuous surface without bumps and depressions. This is typical for *Croizetoceros ramosus* and the genus *Capreolus* from the Middle Pleistocene up to today; therefore the fragmentary MT III of IPUW 7512 DA 26/3/4 offers a valuable diagnostic feature (Fig. 17).

3. In plantar view the transverse articular facies tarsea in contact with the os centroquartalis protrudes beyond the articular surface. It forms a significant peak. In *Eucladoceros* this peak is centered above the sulcus longitudinalis and the canalis metatarsi proximalis (fig. 78A, 2a in PFEIFFER 1999a). In top view on the proximal epiphysis the plantar facies exceeds the canalis metatarsi proximalis minimally (fig.79A, 2a in PFEIFFER 1999a). The transversely directed articular facies tarsea is short.

    In IPUW 7512 DA 26/1/7 as well as in the slightly smaller species from Perrier, probably *Praeelaphus perrieri* (n=5), in plantar view the plantar facies exceeds the sulcus longitudinalis and the canalis metatarsi proximalis slightly, a more axially orientated peak is formed (fig. 78B, 2b in PFEIFFER 1999a), and the facies is somewhat longer than in *Eucladoceros* (Fig. 15, arrow 1). By contrast, in recent cervids of the genera *Cervus* s. str., *Dama* and *Axis* the facies articularis tarsea in contact with the os centroquartalis is elongated, clearly exceeding the canalis metatarsi proximalis in axial direction. In plantar view the peak is directed more

Fig. 16. MT III+IV of IPUW 7512 DA 26/2/7 in plantar view: The transverse articular facies tarsea in contact with the os centroquartalis protrudes beyond the articular surface, clearly exceeding the canalis metatarsi proximalis, ending in a proximally and axially orientated peak (arrow 1). The possible proximal relict of MT II grown together with MT III proximally extends beyond the articular surface in a distinct peak (arrow 2). Both characters occur in *Dama pardinensis* and commonly in the *Dama*-lineage.

1 cm

axially (fig. 78C, 2c; 79C, 2c in Pfeiffer 1999a). This character state is present in IPUW 7512 DA 26/2/7 (arrow 1 in Fig. 16).

4. In addition, in plantar view axially the possible proximal relict of MT II adhered with the proximal end of the MT III ends in a peak in IPUW 7512 DA 26/2/7 (Fig. 16, arrow 2). Schlosser (1886) was one of the first to study in detail Miocene ruminants and demonstrated that relicts of MT II adhered with the MT III form the facet for the cuneiforme I. The excellent drawings in Schlosser (1886, table III) show very primitive metatarsals in which the fusion of MT II+III proximally is still visible. The proximal MT II-relict forms a bulge which surmounts MT III axially, plantarly and proximally. In IPUW 7512 DA 26/2/7 a bulge is also prominent, including the facet for the cuneiforme I. Accordingly, a MT II-relict is possibly preserved in this Pliocene metatarsal, pointing to the primitive development status of this species. This feature is pictured in Croizet & Jobert (1828: pl. 7, fig. 5) for a juvenile cervid from Perrier listed there under the name *Cervus etueriarum*. This taxon was partly assigned to *Cervus pardinensis* by Heintz (1970). This strongly developed peak is probably a plesiomorphic character state.

Results: The morphological analysis of the skeletal features of MT III+IV assigned to IPUW 7512 DA 26/1/7 yields a number of predominantly plesiomorphic character states shared with the Plio-Pleistocene taxa *Eucladoceros*, *Arvernoceros ardei* and *Praeelaphus perrieri*. The characteristics of the facies articularis tarsea in contact with the os centroquartalis is one of the few diagnostic criteria distinguishing these taxa. IPUW 7512 DA 26/1/7 shares the morphology that possibly belongs to *Praeelaphus perrieri*. Croizet & Jobert (1828) picture a hind foot of *Praeelaphus perrieri* from Etouaires (pl. VI, fig. 4), intact from the hind tarsal joint, where a possibly rudimentary MT II is considerably adhered with MT III. The morphology of the MT III+IV of IPUW 7512 DA 26/1/7 corresponds to this primitive development stage. The dimensions of IPUW 7512

Fig. 17. Proximal articular surface of the MT III+IV from IPUW 7512 DA 26/3/4: No peaks or depressions are present axially in the articular surface contrary to plesiometarpal deer (arrow). IPUW 7512 DA 26/3/4 shares this character state with *Croizetoceros ramosus*, *Procapreolus*, and *Capreolus*.

DA 26/1/7 lie in the medium scatter range of *Praeelaphus perrieri* and *Arvernoceros ardei* from Perrier and in the lower scatter range of *Eucladoceros ctenoides* from Senèze (BP: 36–47 mm; TP: 40–50 mm; n=26) and St. Vallier (BP: 40.5–47 mm; TP: 44.5–50.5 mm; n=19) HEINTZ (1970).

The estimated size of IPUW 7512 DA 26/2/7 (TP: 29.5 mm + ca. 5 mm) is consistent with measures given by HEINTZ (1970) for *Dama pardinensis* (Etouaires, Vialette TP: 32.5–37 mm; n=13), and *Dama rhenana* from St. Vallier and Senèze (TP: 30–37mm; n=65). IPUW 7512 DA 26/2/7 is morphologically consistent with *Dama pardinensis* from Etouaires.

IPUW 7512 DA 26/3/4 agrees with *Procapreolus* and *Croizetoceros ramosus* from St. Vallier in morphology and size. The straight, continuous proximal articular surface of MT III without bumps and depressions provides a valuable diagnostic feature (Fig. 17).

Upper and lower teeth

Dama pardinensis

M a t e r i a l : right anterior loph of M^1 or M^2 (IPUW 7512 DA 26/2/1), right M^3 (IPUW 7512 DA 26/2/2), right I_1 (IPUW 7512 DA 26/2/3).

D i m e n s i o n s :

M^1 or M^2: breadth of the anterior loph: 22.3 mm (measured at the crown base)

M^3: maximum length: 19.2 mm, maximum breadth: 20.8 mm.

I_1: maximum breadth of the tooth crown: 12.4 mm, maximum breadth at the crown base: 8.2 mm

D e s c r i p t i o n : The fragment of M^1 or M^2 has a medium degree of wear (Fig. 18). In the M^3 the posterior loph is not worn, the enamel edge is still intact. IPUW 7512 DA 26/2/1/2 corresponds in the dimensions of the preserved M^3 with values of *Dama rhenana* from Senèze and Middle- to Late Pleistocene fallow deer. The incisal edge of the I_1 shows no abrasion. The root is missing.
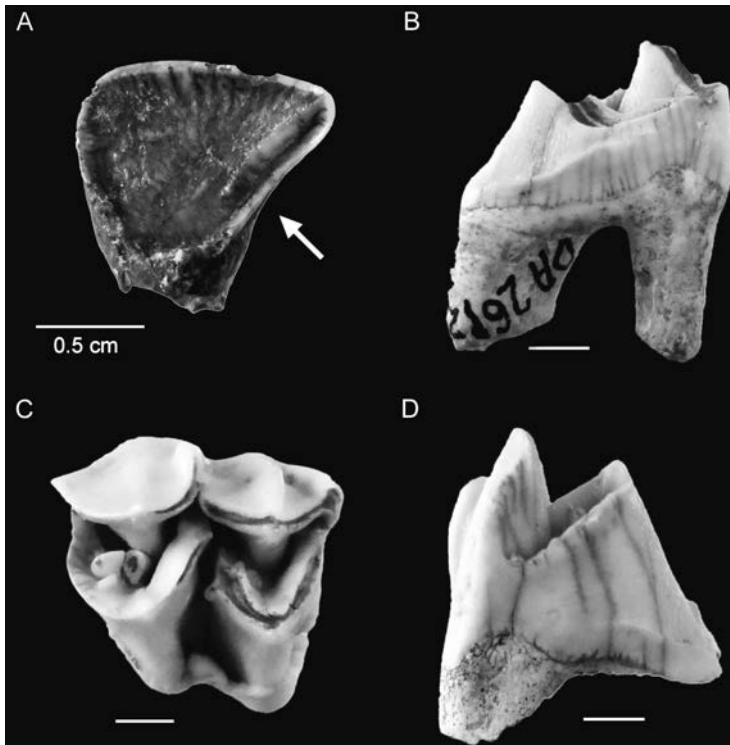
Fig. 18. **A**: right 1st incisive (IPUW 7512 DA 26/2/3), lateral edge of the tooth is strongly bent outwards (arrow), typical for the *Dama*-lineage; **B**: right front loph of M^1 or M^2 (IPUW 7512 DA 26/2/1), note distinct cingulum is developed at the anterior and posterior loph (a plesiomorphic expression); **C–D**: right M^3 (IPUW 7512 DA 26/2/2); C: occlusal view, note almost triangular outline of tooth wall of the anterior and posterior loph and marked peak at hypoconus and protoconus on the M^3; D: posterior view, note deeply carved posterior wall of M^3, a typical character of the *Dama*-lineage. Scale bars equal 0.5 cm.

D i s c u s s i o n   o f   t h e   m o r p h o l o g i c a l   c h a r a c t e r   s t a t e s : At the 1st incisive the crown is especially broadened laterally. From the base to the crown, the lateral edge of the tooth is strongly bent outwards (Fig. 18A arrow). This is typical of the *Dama*-lineage. Based on this feature, *Dama* can be separated from *Cervus* s. str., *Alces* and *Capreolus* (compare fig. 24 in NIETHAMMER & KRAPP 1986). At the 1st incisive the crown of the latter taxa is also broadened, but the lateral edge is not bent outwards. In *Axis axis* (n=18) the 1st incisive is triangular, fan-shaped.

Also the dimensions of the 1st incisive from Deutsch-Altenburg 26 fit with *Dama*.

Morphologically the preserved M^2 and M^3 fit well with Plio-Pleistocene representatives of the *Dama*-lineage. The development of a distinct cingulum on the anterior and posterior loph and the expression of a strong entostyle are plesiomorphic (Fig. 18B, C). The morphology of M^3 IPUW 7512 DA 26/2/2 fits with *Dama pardinensis* from the Pliocene

sites Vialette, Etouaires and Pardines, whereas in *Dama rhenana* from the Early Pleistocene locality Senèze these features can be more weakly expressed, and are further reduced in the Middle- to Late Pleistocene. This emphasizes the gradual evolution of the *Dama*-lineage (see discussion in PFEIFFER 2005).

The posterior wall of M^3 is deeply carved (Fig. 18D). PFEIFFER (1999a, fig. 34, 6a) used this feature to separate fallow deer from red deer. In the *Dama*-lineage the deeply carved tooth wall occurs from the Plio-Pleistocene up until today, but is also present in the Pliocene *Cervocerus novorossiae* and *Praeelaphus perrieri* from Perrier. It may be a plesiomorphic character.

Lingually the tooth walls of the anterior and posterior loph show an almost triangular outline, with a marked peak at hypoconus and protoconus. Labially the mesostyl is very pronounced, forming a fold with the praemetacrista and postparacrista (terminology based on RÖSSNER 1995). Also in these morphological characters the M^3 IPUW 7512 DA 26/2/2 corresponds with Plio–Pleistocene representatives of the *Dama*-lineage. *Praeelaphus perrieri* also shows a strong development of the mesostyle. The outline of the anterior and posterior lingual loph is approximately triangular, but rounded at its base. The length of 19.2 mm, measured from the base of the crown, is clearly lower than values for *Praeelaphus perrieri* (about 23 mm). Therefore *Praelaphus perrieri* can be excluded.

Based on morphology and dimensions, the M^3 from Deutsch-Altenburg 26 reaches the highest correspondence with *Dama pardinensis*.

Mandibula

Croizetoceros ramosus vel. *Procapreolus* sp.

M a t e r i a l : right mandible with P_2–M_2 (IPUW 7512 DA 26/3/2), right mandible fragment with P_2, P_3, P_4, M_1– fragment (IPUW 7512 DA 26/3/3).

D e s c r i p t i o n : Two right mandibles in the size of *Croizetoceros ramosus*, *Procapreolus cusanus* and *Capreolus suessenbornensis* are present (Fig. 19).

The first, better-preserved mandible with tooth row from P_3 to M_2, teeth show a low degree of wear. In the second right mandible with complete P_2, P_3, the anterior part of P_4, and an isolated anterior loph of the M_1, the teeth are significantly worn.

D i m e n s i o n s : see Table 2.

The measured dimensions fit within the range of *Croizetoceros ramosus* from St. Vallier (HEINTZ 1970) and the Middle-Pleistocene roe deer *Capreolus sussenbornenesis* from Mosbach (Table 2).

Remarkable is the high morphological accordance in the dental features between the mandibles from Deutsch-Altenburg 26, *Croizetoceros ramosus* and *Capreolus sussenbornenesis*.

Corresponding characteristics are, on P_3, a strongly developed praeprotoconulidcristid and postprotoconulidcristid, a clearly developed postmetacristid, and the praeentocristid and posthypocristid form a narrow U-shape (terminology based on ROESSNER 1995). The tooth wall labially displays a deep indentation, which is less pronounced in *Capreolus*.

The P_4 shows a typical development of molarising for telemetacarpal deer (see PFEIFFER 1998b). An elongated lingual cingulid connects the anterior edge of the tooth with the metaconid and extends to the entoconid (Fig. 19). An elongated postentocristid extends diagonally to the posterior posthypocristid. The labial tooth wall forms a deep fold. HEINTZ (1970: pl. 21, fig. 3a–3c and pl. 13, fig. 1a–1c) pictures a mandible of *Procapreolus cusanus* and *Croizetoceros ramosus* from Etouaires with exactly corresponding tooth morphology. This morphology is also present in *Croizetoceros ramosus* from St. Vallier and in *Capreolus suessenbornensis* from Mosbach.

The preserved molars show a well-developed cingulum and strong ectostylids. In these expressions the mandibles from Deutsch-Altenburg 26 are conform to *Croizetoceros ramosus* from St. Vallier. From the Pleistocene *Capreolus suessenbornensis* to recent *Capreolus capreolus*, cingula and ectostylids gradually decrease or are totally reduced. The labial tooth wall folded into two triangles with the considerably labially extended

Table 2. Mandible measurements. The measured dimensions of the lower teeth of *Procapreolu*s sp./*Croizetoceros ramosus* from Deutsch-Altenburg 26 fit within the range of *Croizetoceros ramosus* from St. Vallier (adopted from HEINTZ 1970) and the Middle Pleistocene roe deer *Capreolus sussenbornenesis* from Mosbach.

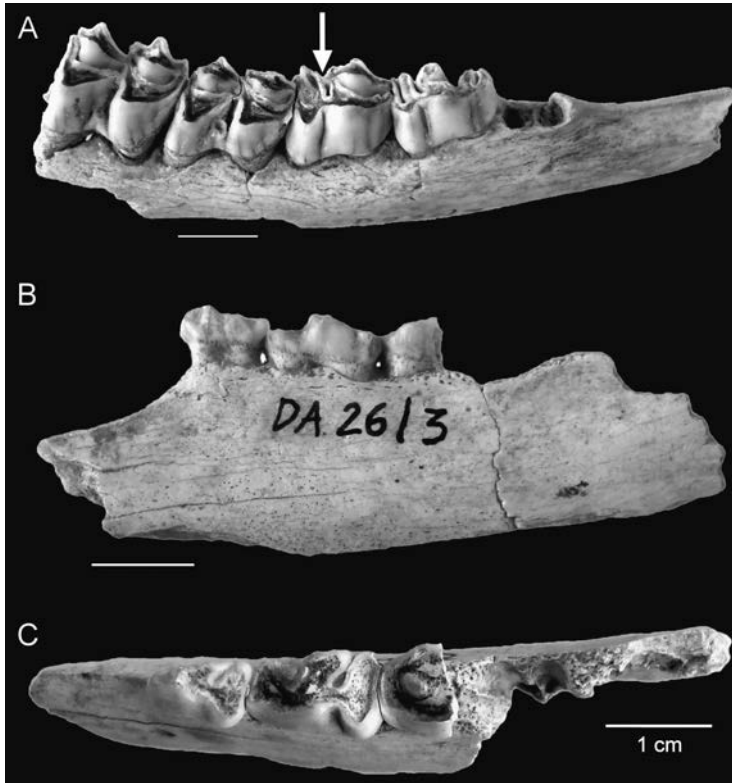| Mandible, *Procapreolus* sp./*Croizetoceros ramosus*, Deutsch-Altenburg 26						
tooth length in mm	P_2	P_3	P_4	M_1	M_2	M_3
n	1	2	1	1	1	
IPUW 7512 DA 26/3/2		11.0	11.3	13	13.1	
IPUW 7512 DA 26/3/3	8.2	11.0				
Capreolus suessenbornensis, Mosbach						
length	toothrow	P_2	P_3	P_4	M_1	M_2	M_3
n	9	13	21	22	27	31	20
Max	77.2	11.5	12.1	13	14	15	19
Min	67.1	7.2	10.1	10.7	11.2	12.8	16.3
x̄	73.01	8.95	11.34	12.05	12.72	13.79	17.68
Croizetoceros ramosus, St. Vallier (HEINTZ 1970)						
length	toothrow	P_2	P_3	P_4	M_1	M_2	M_3
n	9	28	33	38	37	38	37
Max	77.2	9	11.0	12.5	14.5	16	21
Min	67.1	7.5	9	10	11.5	13.5	18.5
x̄	73.01	8.37	10.15	11.25	13.1	14.88	19.63

Fig. 19. Two right mandibles of *Croizetoceros ramosus* or *Procapreolus cusanus* (IPUW 7512 DA 26/3/2 and IPUW 7512 DA 26/3/3): The P_4 displays a typical development of molarisation. The molars have a well-developed cingulum and strong ectostylids. The labial tooth wall of the molars is folded into two triangles. All morphological characters and dimensions agree with *Procapreolus cusanus* and *Croizetoceros ramosus*. Scale bars equal 1 cm.

protoconid and hypoconid. Other examined cervids usually show much more rounded moldings of the anterior and posterior lophs.

R e s u l t s : The studied mandibles belong to *Procapreolus* sp. or *Croizetoceros ramosus* based on tooth morphology and dimensions.

Antler

Cervidae indet.

M a t e r i a l : flattened distal antler tine (IPUW 7512 DA 26/3/1)

D e s c r i p t i o n : The fragment of an antler tine is preserved, with bite marks, and flattened at its base (Fig. 20). The maximum preserved length is 69.2 mm. The diameter at the base is 18.5 mm.

Fig. 20. IPUW 7512 DA 26/3/1 fragment of an antler tine: The back tine is flattened at the base, showing strong bite marks. Such tines are typical for *Croizetoceros ramosus* and *Procapreolus cusanus* but also occur in *Dama* and larger deer species.

A taxonomic assignment is not possible. Terminal tines morphologically identical to IPUW 7512 DA 26/3/1 are common in *Croizetoceros ramosus* and *Procapreolus*. A distinction from *Dama pardinensis* is difficult. Back tines of *Dama* are often roundish in cross-section, but flattened tines also occur. Larger deer species also evolved terminal tines in this shape.

Discussion and conclusions

The distinction between *Arvernoceros ardei* and *Praeelaphus perrieri* from Perrier is well founded on antler morphology but is not entirely satisfactory based on dimensions and morphological characters of the postcranial skeleton. Large overlapping size ranges complicate a separation. Attention has to be paid on a strong sexual dimorphism. *Arvernocervus ardei* seems to exceed *Praelaphus perrieri* slightly in body size based on dimensions of the tooth rows and long bones given in (DEPERET 1884). HEINTZ (1970) could not distinguish these taxa based on teeth.

A restudy of the cervid bone material from Perrier enabled the detection of several morphological characters that might be suitable to distinguish between these species. Distinguishing characters were found on the humerus, the radius, the MC III+IV, the tibia, the MT III+IV and the astragalus. A detailed explanation will be given in a separate study.

Three of these characters could be compared to the material from Deutsch-Altenburg 26. The differing morphology of the cochlea tibiae, of the distal humerus, and the differing degree of fusion of the proximal end of MC III+IV are discussed above in this paper. In medial view the epicondyle of the humerus is merely bordered by a straight edge in *Arvernoceros ardei*, whereas *Praeelphus perrieri* has a distinct depression in the center of the boundary edge in accordance with IPUW 7512 DA 26/1/3 (Fig. 8B). This character state supports the assignment of the humerus IPUW 7512 DA 26/1/3 to *Praeelaphus perrieri*. In palmar view a significant gap occurs proximally in the area where MC III+IV grow together, typical for *Arvernoceros ardei* and *Eucladoceros* in most cases. The MC III+IV are completely adhered in *Praeelaphus perrieri* (Fig. 13). Therefore, some suitable features were detected to distinguish the cervids from Perrier. The comparison with the cervids from Deutsch-Altenburg 26 leads to a more complicated situation because *Eucladoceros* possibly occurred in the fauna.

As shown above in the discussion of the postcranial characteristics, a distinction between *Arvernoceros ardei* and *Eucladoceros* is rarely possible. Solely the distal tibia IPUW 7512 DA 26/1/8 differs in the observed morphology from *Arvernoceros ardei* and is

assigned to *Eucladoceros*. The basic information is poor for *Arvernoceros ardei*. Variation in the tibia character states cannot be excluded.

Based on the diagnostic catalogue for cervids by PFEIFFER (1999a, 2002, 2005) including 122 skeletal, tooth, and antler characters, ninety characters could be compared between *Arvernoceros ardei* and *Eucladoceros*. Skull characters are not available for *Arvernoceros ardei* from Perrier. Seventy two of these characters are similar in both genera. Among the eighteen differences are three character states *Arvernoceros ardei* shares with one species of *Eucladoceros*, *E. ctenoides* or *E. dicranios*. Among the remaining fifteen observed differences, several character states may be plesiomorphic. In *A. ardei* the significant gap proximally in the area where MC III+IV grow together, and the well-developed cingula on the teeth, are certainly plesiomorphic. Most of the observed skeletal character states may be plesiomorphic in both genera, but the conformity is striking. It seems likely that *A. ardei* and *Eucladoceros* are close relatives. *A. ardei* is more primitive than *Eucladoceros* based on its less complex antler morphology, teeth with well-developed cingula, and on several postcranial characters.

In the observed *Dama*-material from Deutsch-Altenburg the narrow trochlea humeri is a significant feature occurring in all *Dama*-species from the Pliocene up to now, separating them from *Cervus* s. str. and *Axis*. Stronger Plio-Pleistocene cervids such as *Eucladoceros* and *A. ardei* approach these species in their trochlea proportions of the distal humerus (Fig. 10) but cannot be confused with *Dama* due to their larger size (Fig. 9). The laterally extremely broadened tooth crown of the first lower incisive together with the outward bending posterior tooth edge is another key-feature of *Dama*, occurring in all *Dama*-species since the Pliocene. The preserved plesiomorphic character states of the metatarsal bones and the strongly developed cingulum on M^2 and M^3 in IPUW 7512 DA 26/2/2 and IPUW 7512 DA 26/2/3 allow an assignment to *Dama pardinensis*.

The main arguments for the occurrence of *Procapreolus* or *Croizetoceros ramosus* in the fauna of Deutsch-Altenburg 26 are the character states of the lower teeth in the preserved mandibles referred to IPUW 7512 DA 26/3/2 and IPUW 7512 DA 26/3/3. All character states are in accordance with *Croizetocerus ramosus* and *Procapreolus cusanus*. The special morphology of the P_4 is shared with Middle Pleistocene to Holocene members of the genus *Capreolus*. It is very similar to those of *Rangifer*, *Odocoileus* and *Alces*, all telemetacarpal deer of much larger body size.

In searching for morphological skeletal characters that support the monophyly of this deer family, PFEIFFER (2000) found a special deepening in the articular surface of the astragalus corresponding with the cubonaviculid (PFEIFFER 2000: fig. 1). This character state has not been found in any plesiometacarpal deer until now. It is also present in rich bone material assigned to *Croizetoceros ramosus* from St. Vallier. Note that the astragali with the deepening may belong to *Procapreolus* sp., a genus which has not been described from St. Vallier so far (GUÉRIN 2007). A second argument for the existence of *Procapreolus* sp. is based on the MT III with its straight, continuous proximal articular surface without bumps and depressions (Fig. 17). It is a valuable diagnostic feature for

Procapreolus and *Capreolus* but seems to also be present in the bone material referred to *Croizetoceros ramosus*. Even if *Procapreolus* is not present in the fauna of St. Vallier, two possibly synapomorphic character states of *Procapreolus*, *Capreolus* and *Croizeto-cerus* suggest a closer relationship of these taxa in addition to the tooth morphology.

Nonetheless, the postcranial skeletal identification of *Croizetoceros ramosus* requires further research. VALLI (2010) reports on another valuable character of telemetacarpal deer on the otic region of the skull, shown in *Procapreolus cusanus* from Perrier-Etou-aires (VALLI 2010: fig. 3). This character should be studied in *Croizetoceros ramosus*. Further research will no doubt shed new light on this question. *C. ramosus* was possibly a telemetacarpal deer.

Acknowledgements

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