Early Pleistocene small-sized deer of Europe

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ABSTRACT: The article presents a systematic revision of early Pleistocene small-sized deer of Europe, their taxonomy, morphology, individual and ontogenetic variation, ecology and evolution. *Cervus nestii* (AZZAROLI, 1947) is the most ancient representative of the "*elaphus* group" and is closely related to the actual red deer. *Dama eurygonos* (AZZAROLI, 1947) and *D. vallonnetensis* (DE LUMLEY *et al.*, 1988) belong to an archaic lineage of fallow deer with simple non-palmed antlers. *Metacervoceros rhenanus* (DUBOIS, 1904) is a primitive deer similar to actual forms of the genus *Axis*. The emended definitions of the species are proposed.

Key-words: Early Pleistocene, Cervidae, taxonomy, morphology, systematics, evolution.

ΠΕΡΙΛΗΨΗ: Στη μελέτη αυτή παρουσιάζεται η συστηματική αναθεώρηση των μικρόσωμων ελαφιών του Κάτω Πλειστοκαίνου της Ευρώπης, η ταξινόμησή τους, η μορφολογία και οντογενετική τους ποικιλότητα, η οικολογία και η εξέλιξή τους. Το είδος *Cervus nestii* (AZZAROLI, 1947) είναι ο αρχαιότερος αντιπρόσωπος της «ομάδας elaphus» και σχετίζεται άμεσα με το αρτίγονο ελάφι. Η Dama eurygonos (AZZAROLI, 1947) και η D. vallonnetensis (DE LUMLEY et al., 1988) ανήκουν σε μία αρχαϊκή εξελικτική γραμμή του Dama dama με απλά μη παλαμοειδή κέρατα. Ο Metacervoceros rhenanus (DUBOIS, 1904) είναι ένα πρωτόγονο ελάφι όμοιο με τις αρτίγονες μορφές του γένους Axis. Προτείνεται αναθεώρηση των ειδών. **Λέξεις-κλειδιά:** Κατώτερο Πλειστόκαινο, Cervidae, συστηματική ταξινόμηση, μορφολογία, εξέλιξη.

INTRODUCTION

Fossil deer represent an important and well-documented back-ground faunal group from the Villafranchian of Europe. However, the systematics of cervids remain confused p a r t l y due to the incomplete original description of species, partly due to the inadequate selection of diagnostic characters. The number of species and subspecies of the so-called smallsized Early Pleistocene deer amounted to ten and the species names in many cases are not supported by a clear definition and differential diagnosis. The unsolved taxonom i c questions caused a simplified and arbitrary approach to deer based on animal's size. Many authors applied the simplistic division of fossil deer into "large-sized deer" (= Me galoceros s. l.) and "small-sized deer" (= D ama-like deer = Cervus s. l.). The arbitrary group of "small-sized deer" includes the forms with estimated body weight below 100 kg. The simplified approach to the fossil deer systematics does not allow the adequate implication of the reach deer material in the biostratigraphic, paleozoogeographic, evolutionary and palaeoecologic studies.

AZZAROLI (1992) attempted to find the systematic position for the small-sized deer and proposed the new genus *Pseudodama*. However, this point of view assumes the broad morphological variation of species included in the genus and generally is based on the small body size of the deer. The further systematic studies (PFEIFFER, 1997; DI STEFANO & PETRONIO, 1998; GIROTTI *et al.*, 2003) results the various opinions on the systematic position of the small-sized deer, but the belonging of all early Pleistocene small-sized deer to a single genus was accepted uncritically. The present paper proposes a new attempt of systematic and taxonomic revision of the so-called "small-sized deer" with the analysis of original descriptions, the revision of holotype morphology, the individual variation and emended diagnoses. The special attention is paid to the cranial morphology that was underestimated and disregarded in the systematic research. The results of systematic revision are applied in the phylogenetic and evolutionary research, the study of ecological adaptations.

MATERIAL AND METHODS

Material studied

The samples of small-sized early Pleistocene deer involved in the present study are stored in the following collections: the Museum of Geology and Palaeontology of the University of Florence (MGUF); the Natural History Museum of London (NHML); Musée de Préhistoire

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régionale du Menton, France (MPRM); Musée National de Histoire Naturelle, Paris (MNHNP); Musée National de Prehistoir les Eyzies de Tayac, Dordogne, France (MNP); the Institute of Zoology of University of Wroclaw (IZUW); the Paleontological Institute, Moscow (PIN); the Paleontological Museum of the University of Lyon (PMUL); the National Museum of Natural History, Kiev (MNHK). The types involved in the systematic revision:

Dama nestii nestii AZZAROLI 1947 (type species); holotype IGF 363 (antlers), MGUF

Dama nestii eurygonos AZZAROLI 1947, holotype IGF 245 (antlers), MGUF

Pseudodama lyra AZZAROLI 1992; holotype IGF 1934V (antlers), MGUF

Pseudodama farnetensis AZZAROLI 1992; holotype IGF 194V (antlers), MGUF

Cervus nesti vallonnetensis DE LUMLEY *et al.* 1988; holotype Nr. 10170 (antler), MPRM.

Cervus warthae CZYZEWSKA 1968; holotype Nr 1, (skull), IZUW.

Cervus (*Cervodama*) *pontoborealis* PIDOPLICZKO & FLEROW 1952; cast of holotype (shed antler), MNHK.

The comparative material on modern deer used in the present work is stored in the Zoological Department of NHML, the Zoological Museum "La Specola" of MGUF, and the Zoological department of MNHNP.

Methods and Terminology

The terminology of dental morphology in ruminants proposed by HEINTZ (1970) and on antler morphology according to LISTER (1990) is followed in the present study. The method of study of cranial morphology by VISLOBOKOVA (1990) with minor modifications is applied in the research. The methodology by JANIS (1990) on body mass prediction is applied for size estimation of fossil deer.

Morphological criteria of a Genus

The attempts of PFEIFFER (1997) and DI STEFANO & PETRONIO (1998) to apply the postcranial morphology in the systematical study of the cervid genera and subgenera gave inadequate results. The limb bones of ruminants influenced by environmental and biomechanical factors during locomotion have a minor interest for the systematic study at the genus and subgenus level. The postcranial morphology depends of the species ecology and locomotion strategy, the landscape character and the body weight (SOKOLOV et al., 1964; GAMBARYAN, 1970; SUTULA, 1990; KÖHLER, 1993). Thus, the possible resemblance between the Villafranchian "Pseudodama" and actual Dama in postcranial morphology may suggest only the similar locomotion strategy and ecological preferences. Hence Euraxis is rather an artificial group that contains the species sharing with the modern Axis the similar ecological adaptations (locomotion type, habitat, body size), but not the real evolutionary

proximity. The cranial morphology (besides the exosomatic parts like the predental portion and preorbital fossae) provides a set of plesiomorphic characters that have a taxonomic value for genus level in the systematics of actual and fossil deer (FLEROW, 1954; SOKOLOV, 1959; VISLOBOKOVA, 1990): 1) the proportions of facial and neural parts of skull; 2) the shape of parietal bones; 3) the shape and relative length of frontal bones; 4) the position, orientation and length of pedicels; 5) the size, position and shape of orbits; 6) the morphology and size of ethmoidal openings; 6) the position and length of nasal bones; 7) the position and shape of the naso-frontal suture; 8) the position of the upper dentition row with respect to orbits; 9) the size and shape of *bulla timpani*; 10) the shape of *basioccipitale*; 11) the morphology and proportions of the lower mandible (shape of processus angularis, the angle between horizontal and ascending portions).

The attempt of MARKOV & DANILKIN (1999) to apply the cranial morphometry in the systematic study of modern subspecies of *Cervus elaphus* gave unfit results that confirm the necessity of proper taxonomic evaluation for characters involved in the systematic research.

The morphology of dentition and antlers are more widely used in the systematic research and various authors suggested the following characters as morphological criteria at the genus level (FLEROW, 1952, 1962; HEINTZ, 1970; VISLOBOKOVA, 1990; AZZAROLI, 1992): 1) the angle between labial and lingual slopes of upper molars, which is correlated with tooth crown height; 2) the presence or absence of upper canines.

The antler morphology traditionally is applied in the cervid genera description (PIDOPLICZKO & FLEROW 1952; HEINTZ, 1970; AZZAROLI, 1992). The implication of antler morphology in the systematics of genera is restricted only to the general plan of antler construction observed in several species.

Morphological criteria of a Species

The species description is based on the exosomatic characters that depend of the certain ecological niche of species (FLEROW, 1954; SOKOLOV, 1959; VISLOBOKOVA, 1990; AZZAROLI, 1992). The cranial and dental characters of the species rank are the following: 1) the relative length of the predental part and the correlated length of dia s t e m a; 2) the shape of premaxillary bones; 3) the length of naso-premaxillar suture; 4) the size and degree of development of preorbital fossae; 5) the shape of frontal appendages (pedicles); 6) the development of cingulum, *Paleomeryx* fold and other additional enamel folds; 7) the ratio between premolar and molar tooth series length; 8) the molarisation of lower fourth premolar (P_4).

JANIS & LISTER (1985) described a rather high individual variation of P_4 in pecorans and suggested a cautious implication of this character in taxonomy studies. The high morphological variation of P_4 is shown for *Cervus* *elaphus* with frequency of low molarisation from 8 % to 47 % in different populations. GUADELLI (1987) used the simple morphology of P_4 as an argument defining a subspecies of red deer *C. elaphus simplicidens* from Western France. Apparently, P_4 is rather variable in Cervinae, although the high molarisation of P_4 seems to be rather constant in the genus *Dama*. This character is more constant also in the deer of Odocoileinae group. The characters of antler morphology used in the species systematics: 1) the direction, shape and length of the antler beam; 2) the number of times; 3) the development of palmation.

The proportions of limb bones and body size are used in the species definition only in combination with the above mentioned characters.

Morphological criteria of a subspesies

As a rule, the subspecies criteria are details of antler and dental morphology and body size. In the case of polymorphous species, the development of antler palmation, the relative length of predental part of the skull, the degree of molarisation of P_4 , the development of entostyles and *Palaeomeryx* fold are used as characters defining subspecies (HEPTNER & TZALKIN, 1947; ABBAZZI, 1995; GUADELLI, 1987; CROITOR & STEFANIAK, in press).

SYSTEMATIC DESCRIPTION

Subfam. Cervinae BAIRD, 1857 Genus Cervus L. (= Pseudodama Azzaroli, 1992, = Euraxis DI Stefano & PETRONIO, 1998) Cervus nestii (Azzaroli, 1947)

Synonymy:

1879 Cervus nestii nomen nudum: FORSYTH MAJOR, p. C
1947 Dama nestii nestii (F. MAJOR): AZZAROLI, p. 54, fig. 4 (4)
1992 Pseudodama lyra sp.nov.: AZZAROLI, p. 6, Fig. 2, pl. 1, fig. 1 a-c
1992 Pseudodama nestii (AZZAROLI): AZZAROLI, p. 12, figs 5-7
1997 Dama (Pseudodama) nestii (AZZAROLI): PFEIFFER, p. 34
1998 Euraxis lyra (AZZAROLI): DI STEFANO & PETRONIO, p. 52
1998 Euraxis nestii (AZZAROLI): DI STEFANO & PETRONIO, p. 52
2003 Axis nestii (AZZAROLI): GIROTTI et al., p. 88, fig. 3a-d

Original citation:

FORSYTH MAJOR'S (1879, *n.v.*) original citation of the species name *Cervus nestii* was not accompanied by a species description, a type designation and a describing figure (*fide* AZZAROLI, 1992). AZZAROLI (1947) proposed the description of subspecies *Dama nestii nestii* F. MAJOR and figured of type specimen. Later, AZZAROLI (1992) considered FORSYTH MAJOR'S *Cervus nestii* as *nomen nudum* and suggested that the authorship of the species "*nestii*" belongs to AZZAROLI (1947). The formal diagnosis of the species was not proposed. The species name "*nestii*"

is used here sensu AZZAROLI (1992).

Diagnosis:

A medium-sized deer. The braincase is unflexed with flattened parietal bones. The facial portion of skull is relatively long: the orbito-frontal region of skull is elongated as in Cervus. The anterior edge of orbit does not reach the level of M². The posterior edge of nasal bones does not reach the line connecting the anterior edges of orbits. The predental part is shorter than upper tooth row. Pedicels are long and sloped from the face toward the posterior. Frontal bones are flat. The lower mandible has more open angle between horizontal and ascending parts, if compared to Dama. The angle between labial and lingual sides of upper molars is comparatively narrow and amounts to 30°. The morphology of P₄ is primitive. Antlers are fourpointed and thin, with comparatively smooth surface. The first (brow) tine is situated at a certain distance from the burr. The middle (trez) tine is well-developed. The distal bifurcation is oriented in the frontal plane. Metapodial bones are short. The metacarpus is shorter than radius.

Holotype:



Fig. 1. *Cervus nestii* (AZZAROLI, 1947): A) the frontal view of holotype IGF 363; B), the frontal view of specimen IGF 1934V (the type specimen of *Pseudodama lyra* AZZAROLI 1992). Adapted from AZZAROLI, 1992.

 TABLE 1

 The relative height of pedicels in Villafranchian deer of Central Italy.

 Legend: d lat-med – latero-medial diameter of pediculum;

 h pedic – medial height of pediculum.

specimens	d lat-med	h pedic	ЪVđ
D. eurygonos, IGF 244 (dx)	35,5	15	42,2
D. eurygonos, IGF 244 (sin)	34,3	15	43,7
"P." farnetensis, holotype 13962 (dx)	38	22,5	59,2
"P." farnetensis, holotype 13962 (sin)	39,8	19,2	48,2
"P." lyra, holotype IGF 1933v, t (dx)	25,7	25	97,3
"P." lyra, holotype IGF 1933v, t (sin)	24,7	27,4	110,9
C. nastii, holotype IGF 363 (dx)	27,1	22,5	83
C. nestii, holotype IGF 363 (sin)	27,5	19,8	72
C. nestli, IGF 289 (dx)	30	25,6	85,3
C. nestli, IGF 289 (sin)	33,3	22,8	68,4
C. nestli, IGF 243 (dx)	28,4	20,3	71,5
C. nestli, IGF 243 (sin)	25,2	24	95,2
L			

A pair of antlers with pedicels and frontal bones IGF 363, MGUF. The major part of the left antler is restored.

Type locality:

Tasso, Upper Valdarno, Central Italy.

Distribution:

Middle Villafranchian – early late Villafranchian, late Pliocene – early Pleistocene; Italy.

Description of holotype.

The type specimen IGF 363 (Fig. 1A) belongs to a mature individual. The antlers are thin, long and four-pointed. The antler surface is smooth, without pearling and deep longitudinal furrows and ribs. The first tine is situated at a certain distance from the burr. The first segment of the beam (the portion between first and second tines) is somewhat longer than the second segment (the beam portion between the second time and the distal bifurcation). The angle of divergence between the first segments of antlers is about 80°. The distal bifurcation is formed by two short tines of almost equal size and is oriented in a frontal plane. The length of the right antler is about 710 mm. Pedicels are comparatively long (Fig. 2, Tab. 1), slightly compressed antero-posteriorly and pointed toward the posterior. The breadth of skull behind pedicels is 104.3 mm.

The antlers IGF1934v from Ponte a Elsa.

The specimen presents a complete pair of antlers with pedicels (Fig. 1B). The antler morphology of the deer from Ponte a Elsa resembles *C. nestii*. The first tine springs off



Fig. 2. The relative length of pedicels in Villafranchian deer from central Italy.

rather high above the burr and forms with the beam an angle of 70°. The measurements of antlers are published by AZZAROLI (1992). The angle of divergence between first segments of the antler beams is of 100° . The first segment portion of antler is rather long. The distal portion of beam above the second tine is short, curved inward and slightly compressed antero-posteriorly. The tip of the right antler is sharp, while the top of the left antler is ended by two small prongs oriented in a frontal plane. The length of right and left antlers amounts to 73 cm and 78 cm respectively. The antler surface is rather smooth. The pedicles are longer than in the type specimen of *C. nestii*. The breadth of skull behind pedicels amounts to 108.0 mm.

AZZAROLI (1992) described the fine antlers from Ponte a Elsa as a new species Pseudodama lyra in the composition of the Triversa faunal unit. AZZAROLI (1992) interpreted the deer from Ponte a Elsa as a transitional evolutionary stage between Villafranchian deer of the pardinensis-rhenanus type with three-tined antlers and Pseudodama nestii with four-tined antlers. Later, DE VOS et al. (1995) suggested P. lyra to be a junior synonyme of Metacervoceros rhenan u s (=Cervus rhenanus: DE VOS et a l., 1995). However, there are some certain differences in antler morphology between the specimen from Ponte a Elsa and M. rhenanus. The antlers of *M. rhenanus* are richly sculptured by pearling and longitudinal ribs and furrows, the apical tine is always cylindrical and its dorso-ventral compression never has been observed, the antler beams are less diverged and not bent inward. The asymmetry of the distal portions of the antlers from Ponte a Elsa suggest a certain instability of this character. The relatively long pedicles may suggest that the antlers from Ponte a Elsa belong to a young individual and represent the early ontogenetic stage of antler development of C. nestii (Fig. 2, Tab. 1).

The skull IGF 243 from Figline.

The antlered skull (Fig. 3, Tab. 2) is laterally crushed and

distorted. Nasal bones are partially destroyed. The skull



Fig. 3. *Cervus nestii* (AZZAROLI, 1947) from Figline: the skull IGF 243, lateral view.

belongs to a young adult individual with fully erupted permanent dentition. The first tine and distal part above the second ramification are destroyed in both antlers. AZZAROLI (1992: p.16, Pl. 6, Fig. 2) published figures of the skull from

 TABLE 2

 Cervus nestii (AZZAROLI, 1947): measurements of the skull IGF243 from Figline.

Measurements	mm
Cranium	
Condylobasal length	250.0
Length of upper tooth row P ² -M ³ (sin)	80.3
Length of upper molars M ¹ -M ³ (sin)	48.1
Length of upper premolars P ² -P ⁴ (sin)	36.0
Distance P ² prostion (predental length)	74.6
Distance M ³ _occipital condyles	96.7
Width before pedicels	92.9
Width behind pedicels	79.3
Maximal width of basioccipitale	37.0
Face length (orbit - prastion)	153.0
Length of braincase behind pedicels	74.7
Mandible (dx)	
Length of tooth row P2-M3	89.4
Length of premolars P2-P4	35.0
Length of molars M1-M3	54.4
Length of horizontal ramus	~215.0
Length of diastema P2-C	52.5
Distance between P2 and foramen mentale	35.1
Mandible height under P2	22.2
Mandible height under M_1	23.2
Mandible thickness under M1	12.6
Height of articular incision	67.3

Figline and described its state of preservation. The detailed morphological description of this specimen is proposed here.

Antlers

Antler beams are thin and gently curved. The antler surface is smooth. The shape of antler base is circular. The first ramification is situated at a short distance from the burr (36.0 mm). The antero-posterior diameter of antler above the burr amounts to 33.4 mm.

Skull

The parietal and frontal bones are flat. The orbito-frontal



Fig. 4. Cranial proportions in fossil and actual deer (males): the relative length of face (%) measured from orbit to *prostion* with respect to the condylobasal length. Data on *C. elaphus bactrianus* and *C. elaphus maral* are adapted from HEPTNER & TZALKIN (1947).

region of skull is rather long: the anterior edge of orbit does not rich M². The posterior edge of nasal bones does not go behind the line connecting anterior edges of orbits. The relatively long pedicels slope backward from the face; the angle between pedicle and parietal bones amounts to 83°. The eye sockets are of moderate size. The preorbital fossae are deep and well developed. The ethmoidal openings are of moderate size. Nasal bones have a very short contact with ethmoidal openings (shorter than 1/2 of the ethmoidal opening length). The length of naso-premaxillar contact is moderate. The upper tooth row is relatively long. The facial part measured from the anterior edges of orbits to the anterior tip of premaxillary bones (prostion), is particularly long and consists 61.2% of the skull length (Fig. 4). The face of C. nestii is relatively longer than in Dama dama, Axis porcinus, C. nippon and slightly longer than in C. elaphus corsicanus. The relative length of face of the specimen under study is close to the actual subspecies of red deer C. elaphus bactrianus and C. elaphus maral. The predental part of C. nestii measured from P^2 to prostion is relatively short (shorter than the length of upper tooth row) that contrasts with the elongated face of this deer (Fig. 5). The short predental portion is also characteristic of C. nippon and C. elaphus bactrianus.



Fig. 5. Cranial proportions in fossil and actual deer: the relative length of predental part (%) measured from P^2 to *prostion* with respect to the upper tooth row length.



Fig. 6. *Cervus nestii* (AZZAROLI, 1947) from Figline: the right hemimandible of the skull IGF 243.



Fig. 7. Mandible proportions of fossil and actual deer: the relative length of diastema (%) with respect to the lower molar series length.

Lower Mandible

The lower jaw of the skull IGF 243 (Fig. 6, Tab. 2) is characterised by an oblique angle between its horizontal and ascending parts, which amounts to 108.5A. The sloped backward ascending part of mandible is correlated with the elongated orbito-frontal portion of skull. The *corpus mandibulae* is slender. The *processus angularis* is stronger developed than in *C. elaphus*. The diastema is comparatively short and amounts to 96.5 % of the molar series length. The relative length of diastema of *C. nestii* is similar to *C. nippon* (92.8 %) and shorter than in *A. porcinus* (117.8 %) and *C. elaphus* (115.8 %) (Fig. 7).



Fig. 8. Cranial remains of small-sized deer from Tasso, Upper Valdarno: A, the fragment of skull IGF289 *Cervus nestii* (AZZAROLI, 1947); B, the fragment of skull IGF244 of *Dama eurygonos* AZZAROLI 1947.

Dentition

The morphology of molars is rather advanced. Upper molars have the weak trace of cingulum with a small entostyle. There are no additional enamel folds in upper molars. The angle between labial and lingual slopes of upper molars amounts to 30°. Lower molars are supplemented with an ectostylide. The *Palaeomeryx* fold is not developed. The P_4 is simple. Its parastylide and paraconide are not clearly separated; the metaconide is simple and rounded; entoconide is directed obliquely toward the posterior. The lower premolar series amounts to 64.3% of the molar series length. The relative length of lower premolars is similar to actual *Cervus*.

The skull IGF 289 from Tasso, Upper Valdarno.

The fragment of antlered cranium (frontal and parietal parts) belongs to a some-what older individual that may be concluded from the obliterated bone sutures. It is characterised by comparatively long and sloped backward pedicels (Fig. 8). The parietal and frontal bones are flattened. The portion of neurocranium behind pedicels is comparatively long. The frontal breadth before pedicels amounts to 101.6 mm; the breadth of braincase behind pedicels amounts to 82.0 mm. The pedicels are long and sloped backward from the face. The first tine of antler springs off at a certain distance from the burr. The antler surface is smooth. The antler burr is normally developed.

The articulated limbs.

The articulated limb bones of C. nestii were briefly described

and figured by AZZAROLI (1992). Here is proposed a detailed description.

Forelimbs (Tab. 3)

The specimen IGF 394 (*dx*) consists of articulated *radius*, *os carpi radiale*, *os carpi intermedium*, *os c ar p a le quadrum*, *os carpale secindum/tertium*, *metacarpus* (AZZAROLI, 1992: Pl. 9, Fig. 4). The forelimb is characterised by relatively short metacarpus that amounts to 92.5 % of the radius length (Fig. 9). The proximal end of radius is comparatively broad. The lateral portion of proximal articulation surface of radius and the *epicondylus lateralis* are narrowed. In its turn, the medial portion of the proximal articulation surface is enlarged and the *epicondylus medialis* is prominent in the frontal view (Fig. 10). The incision for articulation with *processus coronoideus* of ulna is very deep.

The distal end of metacarpus is sharply broadened and the distal epiphysis has a triangular shape. The transversal cross-section of the distal portion of diaphysis shows that the metacarpal shaft is laterally compressed and deep (Fig. 10).

Hindlimbs (Tab. 4)

The specimen IGF 393 (dx) consists of *calcaneus*, *talus*, *cubonaviculare*, *metatarsus*, and the complete set of phalanxes (AZZAROLI, 1992: Pl. 9, Fig. 6). The *metatarsus* is short with relatively wide proximal epiphysis, which has almost circular outlines (Fig. 11). The distal end of *metatarsus* is strongly broadened. The length ratio between *calcaneus* and *metatarsus* amounts to 38.8% and is close to the same index of the actual *C. elaphus* (39.3%). The proximal phalanxes are long and robust, while the medial phalanxes are relatively small. Hoof phalanxes are sharp and long. The postcranial proportions of *C. nestii*, with exception of unusually long and robust first phalanxes, are very close to modern *C. elaphus*.

Ontogenetic variation.

The basal (brow) and middle (trez) tines appear at the early ontogenetic stages of antler development as in the specimen IGF 1934v from Ponte a Elsa. Apparently, the antlers of *C. nestii* from Ponte a Elsa correspond to two –or three– years old stags of the actual *C. elaphus* and *C. nippon*. The antlers of young males of *C. elaphus* and *C. nippon* are characterised by a well-developed trez tine and a short second segment without crown tines (SOKOLOV, 1959; WOLF, 1986). The occurrence of small bifurcation in the one of the antlers of the juvenile individual from Ponte a Elsa, most probably, has an occasional character. The distal fork appears in the fully grown antlers of mature individuals.

Individual variation.

The morphological variation that has an individual character is observed in the height of the first tine insertion. It varies from 36 mm in the specimen IGF 289 to 70 mm in the

TABLE 3 Measurements of articulated forelimbs of small-sized deer from Upper Valdarno.

Measurements (mm)	C. nestii, IGF394	D. eurygonqs, IGF397
Humerus		- L .
Width of distal trochlea humeri		38.3
Diameter of medial lip of trohlea humeri		28.3
Diameter of lateral lip of trochlea humeri		17.8
Radius		
Bone length	213.0	216.0
Width of proximal epiphysis	43.1	40.0
Width of proximal articulation surface	39.2	34.8
Depth of proximal epiphysis	18.0	18.8
Width of distal epiphysis	36.5	37.7
Depth of distal epiphysis	28.2	28.7
Metacarpus		
Bone length	197.5	213.0
Width of proximal epiphysis	28.3	29.1
Depth of proximal epiphysis	21.0	20.6
Width of distal epiphysis	28.6	30.3
Diameter of distal articulation trochlea	19.0	20.8
Phalanx proximalis		lateral
Bone length		46.4
Width of proximal epiphysis		15.3
Depth of proximal epiphysis		19.7
Width of distal epiphysis		13.1
Depth of distal epiphysis		19.7
Phalanx media		lateral
Bone length		27.1
Width of proximal epiphysis		13.2
Depth of proximal epiphysis		18.3
Width of distal epiphysis		10.3
Depth of distal epiphysis		16.0

TABLE 4

Measurements of articulated hindlimbs of the small-sized deer from Upper Valdarno.

Msanzmania (mm)	C. neutl, ICE7 393	D.curygonar, IGF 199
Talus		
Bone length	40.0	41.1
Distal width	25.0	25.4
Distal depth	19.2	20.1
Calcanese	······································	
Hone length	85.4	
Length of tuberonity	56.5	
Width of distal end of tuberosity	18.0	
Cubongviculare		
Bane width	32.0	31.7
Bone depth	26.8	27.1
Metatanetu		
Bone kngth	220.0	243.0
Width of proximal epiphysis	28.5	27.7
Depth of proximal spiphysis	30.4	31,2
Width of distal opiphysis	31.5	30.3
Diameter of distal articulation treahles	21,0	21.6
Phalana proximalis	lateral	Internal
Bone longth	50.2	43.5
Width of proximal epiphysis	16.5	14.5
Depth of proximal epipitysis	20.6	18.2
Width of distal spiphysts	14.2	13.0
Phalan: media	lateral	lateral
Bone length	30.0	29.0
Width of proximal opiphyris	14.6	14,4
Depth of proximal epiphysis	21.3	17.7
Width of distal epiphysis	11.6	11.3
Pholone distalis	Interal	
Bons length	35.0	<u> </u>
Bono height	19.5	



Fig. 9. Proportion of forelimb in fossil and accrual deer: the ratio between metacarpus and radius.



Fig. 10. Atriculated limb bones from Tasso, Upper Valdarno: the proximal end of radius (A) and the distal end of metacarpus with transversal section of diaphysis (B) of *Dama eurygonos* (IGF 397, *sin*); the proximal end of radius (C) and the distal end of metacarpus with transversal section of diaphysis (D) of *Cervus nestii* (IGF 394, *dx*) (all skeletal elements are figured in frontal view). Note the difference in *epicondylus lateralis* shape, depth of incision for *processus coronoideus* (indicated by arrows), shape of distal epiphyses and transversal section of diaphysis between the compared deer (see text).

specimen IGF1934v. Both fossil remains belong to young individuals. The difference in antler divergence between the type specimen and the antlers IGF1934v can not be taken in consideration, as the holotype of C. nestii is broadly restored.

Systematic position of C. nestii (AZZAROLI, 1947).

AZZAROLI (1947) regarded the species under study as an ancent fallow deer. Later, AZZAROLI (1992) designated



Fig. 11. Metatarsal bones of small-sized deer from Tasso, Upper Valdarno (frontal view and proximal articulation surface): A, *Dama eurygonos* AZZAROLI 1947 (IGF 399, *dx*); B) *Cervus nestii* (AZZAROLI, 1947) (IGF 393, *dx*).

Dama nestii nestii as a type species of the genus Pseu dodama, which was considered close to the modern genera Axis and Dama. AZZAROLI (1992) attributed also to the new genus the species Cervus pardinensis, C. rhenanus (= C. philisi), C. perolensis and two new species Pseudodama lyra AZZAROLI 1992 and P. farnetensis AZZAROLI 1992. DE Vos et al. (1995) ascribed the species with three pointed antlers (pardinensis and rhenanus) to the genus Cervus, while the species with four-pointed antlers (nestii and farnetensis) are retained to belong to the genus Pseudoda ma. PFEIFFER (1997) regarded AZZAROLI's Pseudodama as a subgenus of the genus Dama, taking in consideration mostly the morphology of postcranial bones. DI STEFANO & PETRONIO (1998) created the new genus Euraxis with type species Dama nestii nestii (a synonym of Pseudodama) for the Villafranchian small-sized deer and suggested their close relationship to the actual Asian Axis. Surprisingly, the affinity with Axis was also concluded from the postcranial morphology. CROITOR (2001) restricted the genus name Pseudodama only to the type species. In fact, Axis and Dama are morphologically very distant each from another, a fact that brings a contradiction in the definition o f Pseudodama. Unlike Dama, C. nestii is characterised by the rather long and unflexed braincase with flat parietal bones, the comparatively long pedicles some-what sloped

backward from the face, the relative long face with particularly orbito-frontal part, the narrow nasal bones that do not reach behind the line connecting the anterior edges of orbits and the small ethmoidal opening that is limited by the nasal bone at a comparatively short distance, the primitive P₄ and more high crowned molars. Unlike Axis, C. nestii is characterised by the longer face, the shorter pedicles and the four-tined antlers. The cranial morphology of C. nestii and especially the peculiar long face and shape of facial bones and bone sutures is similar to modern C. elaphus. The upper molars lacking hypoconal fold also approach C. nestii to C. elaphus. The cleft lingual wall of P^4 characteristic of C. nestii is occasionally present in the modern red deer as well. C. elaphus shows a stronger affinity in cranial morphology with C. nestii than with C. nippon (Fig. 4). In my opinion, this is a good argument for including AZZAROLI'S Dama nestii nestii in the genus Cervus sensu stricto and to regard the genus name Pseudodama as a junior synonym of Cervus. Antlers of C. nestii show a great affinity with actual forms of red deer C. elaphus barbarus BENNETT from North Africa and C. elaphus corsicanus ERXLEBEN from Corsica and Sardinia, which are characterised by four-pointed antlers with only one basal (brow) tine and frontally oriented distal bifurcation. The antlers of the first true red deer subspecies C. elaphus acoronatus BENINDE and the primitive modern subspecies C. elaphus bactria n u s LYDEKKER have the additional bez tine, however they maintain the similar distal fork oriented in the frontal plane. It is very important to mention that C. elaphus bactrianus is characterized by the shortest predental part of the cranium among the modern subspecies of red deer (HEPTNER & TZALKIN, 1947; FLEROW, 1952) that approach the Bactrian red deer to C. nestii. Thus, C. nestii should be regarded as one of the earliest representative of the "elaphus" group.

Cervus abesalomi KAHLKE 2001

Synonymy:

1995 Cervus perrieri (CROIZET & JOBERT): VEKUA, p. 119, tab. 39, fig. 1 1995 Cervus (Dama) cf. nestii (MAJOR): VEKUA, p. 124, tab.

44, fig. 3

2001 Cervus abesalomi sp. nov.: KAHLKE, p. 475

Description:

The species was described from the Pliocene – early Pleistocene deposits of Dmanisi, Georgia. The holotype is a complete left antler with a fragment of frontal bone (Fig. 12). The antler morphology displays a great affinity with *Cervus nestii* from Italy. The antlers are four-pointed, with high insertion of the first tine. The second (middle tine) divides the antler beam into a longer proximal segment and a shorter distal segment. The antler is terminated by a transversally oriented fork composed by two equal-sized tines. The antler length is about 740 mm. The pedicle length

is equal to the pedicle diameter. The lengths of upper and lower cheek tooth series exceed the measurements of *C. nestii* from Upper Valdarno. The lower premolar series of *C. abesalomi* is comparatively longer (66.6-73.6%) than in *C. nestii* (64.3%). The upper molars maintain the hypoconal fold missing in *C. nestii*. Those dental characters may suggest the deer from Caucasus as a comparatively primitive form, however, the observed differences in dental morphology may present an intraspecific variation and the possible synonymy of *C. nestii* and *C. abesalomi* is not excluded. KAHLKE (2001) regarded *C. abesalomi* as a form evolutionary very close to modern *Cervus elaphus*.

Phylogenetic relationships of Villafranchian Cervus

The understanding of phylogenetic relationships within the genus *Cervus* and the origin of modern red deer is difficult due to the broad variety of modern and fossil forms attributable to the so-called "*elaphus*" group. Apparently, *C. nestii* is the earliest known representative of the "*elaphus*" group that already shows the basic primitive plane of antler morphology of the *elaphus* type and the peculiar elaphine cranial morphology. *C. abesalomi* seems to be a form closely related to *C. nestii*, but some-what more primitive in dentition morphology. However, the Villafranchian *Cervus* from Italy and Georgia may not represent the direct ancestral form of the "*elaphus*" group. The analysis of DNA sequence



Fig. 12. *Cervus abesalomi* KAHLKE 2001: the antler D.1495 from Dmanisi, Georgia, holotype (adapted from Vekua, 1995).

variation of the mitochondrial cytochrome b gene of modern populations of red deer (LUDT et al., 2003) gave the interesting and exciting results on the origin and phylogeny of Cervus elaphus that may be helpful in the interpretation of the paleontologic record. According to LUDT et al. (2003), Central Asia and Tarim region are the area of origin of the genus Cervus where the primordial forms C. elaphus bactrianus LYDEKKER and C. elaphus yarkandensis BLAN-FORD come from. This conclusion is very interesting in the context of the cranial proportions affinity between the Bactrian red deer and the Villafranchian C. nestii. Perhaps, the first expansion of Cervus s.s. in Europe took place during the middle-late Villafranchian. The first elaphine immigrant C. nestii could give a start for radiation of various forms in the Mediterranean area that characterised by antlers with a single brow tine and unusually branched or palmed distal portions. Those endemic descent forms discovered in Italy are C. elaphus aretinus AZZAROLI with branched distal part of antler and very long braincase (AZZAROLI, 1961; DI STEFANO & PETRONIO, 1992) and C. elaphus palmida ctyloceros DE STEFANO with palmed antlers (ABBAZZI, 1995). C. elaphus simplicidens GUADELLI from late Pleistocene of South-West France may also represent a primitive survivor from the peripheral faunal refugia. Perhaps, those archaic forms of the *elaphus* group were absorbed by the new wave of red deer expansion (C. elaphus acoronatus BENINDE) during the beginning of middle Pleistocene.

The Modern fauna of Western Mediterranean still contains a peculiar form of red deer. This is a rather smallsized C. elaphus barbarus BENNETT with primitive antlers similar to C. nestii and white spots on its body. C. elaphus corsicanus ERXLEBEN from Corsica and Sardinia is similar to the Atlas stag and supposed to be introduced on the islands by humans (REUTERSHAN et al., 1999). The modern African red deer C. elaphus barbarus poses many questions. GEIST (1987) considered the Atlas stag as the most primitive form of C. elaphus. Later, GEIST (1998) regarded the Atlas and Corsican stags as pedomorphous isolated subspecies that acquired the primitive characters due to the regressive evolution. LUDT et al. (2003) obtained a surprisingly high genetic differentiation of the Atlas stag together with the Corsican deer from the rest subgroups of the modern red deer with the time of divergence cca. 2.2 Ma (since the middle Villafranchian). Such a significant time of divergence was supposed as a possible overestimation (LUDT et al., 2003). However, the archaic morphology of Atlas and Corsican deer and their genetic segregation may be regarded as a evidence for a long-term isolation of primitive red deer in the Atlas refugia where for the long period maintained rather constant conditions similar to the Pliocene environment of Central Asia. Thus, one can assume that the Atlas stag is a Villafranchian survivor since C. abesalomi and C. nestii arrived in the Ponto-mediterranean Area.

Cervus reihenaui KAHLKE 1996 (= Cervus elaphoides

KAHLKE 1960) from the early Middle Pleistocene of Mosbach rises new questions in the context of the early evolution of the "elaphus" group discussed here. The complete antlers of this species are not known, although KAHLKE (1960) quotes a drawing of the lost complete antler with two basal tines (brow and bez) and the distal fork, missing the trez (middle) tine. The antler construction reminds the basic pattern of the "elaphus" type of antlers with the exception of the missing trez tine, however it does not correspond to the fully grown antlers of C. nestii and primitive forms of C. elaphus. LISTER (1990) suggested that the antlers ascribed to C. elaphoides (= reichenaui) belong to juvenile individuals of C. *elaphus acoronatus*, while the part of teeth and postcranial bones belong to Dama. PFEIFFER (1997) considered the deer under discussion as a valid species and regarded it as a fallow deer Dama (Pseudodama) reichenaui. This conclusion was based mainly on the morphology of the isolated limb bones, which are not clearly associated with the "C. reihenaui" antlers. The unshed antler 61/1054 from Mosbach reported by PFEIFFER (1997: p. 36, Fig. 2) as Dama (Pseudodama) reichenaui, is characterised by a very long pedicle. Such a long pedicle (58 mm) oriented rather obliquely on the frontal bone rules out the belonging to the genus Dama. Obviously, this specimen belongs to a young individual of C. elaphus as LISTER (1990) has proved already.

Ecology of Cervus nestii

The explanation of such specialization in cranial morphology of C. nestii as the long face is difficult. SPENCER (1995) suggests the lengthened face as an adaptation for grazing. However, the long face of C. nestii is combined with long and primitive premolars and short predental portion of the skull, which are characteristic of browsers. The broad epiphyses of long limb bones, the sho r t metapodials and lengthened robust phalanxes of C. nestii are the typical adaptation to the saltatorial locomotion in wooded and mountainous landscapes. The broadened limb epiphyses ensure the limb articulations stability during saltations (EGOROV, 1955; GAMBARYAN, 1972). Apparently, the deep incision for the processus coronoideus on the proximal end of radius is another adaptation for stability of the elbow joint that was exposed to high dynamic load during the saltatorial locomotion. The short metacarpal with increased depth of distal portion of diaphysis in C. nestii may present a biomechanical adaptation to the sagittal breaking forces in mountainous conditions (fide EGOROV, 1955). The large robust proximal phalanx and the strong middle phalanx with prominent plateau postarticulaire are characteristic of woodland dwellers (KÖHLER, 1993). The adaptation of the late Villafranchian Cervus to wooded and m o u ntainous landscapes is supported by the geography of fossil finds that includes the mountainous area of Italy and Georgia.

Genus *Dama* FRISCH 1775 *Dama eurygonos* AZZAROLI 1947

Synonymy:

1947 Dama nestii eurygonos ssp. nov.: AZZAROLI, p. 56, fig. 5 (1) 1987 "Dama" cf. nestii (AZZAROLI): DE GIULI, p. 20, pl. 8-13 1992 Pseudodama nestii (AZZAROLI): AZZAROLI, p. 16, fig. 5.

1992 I seudodama nesta (AZZAROLI). AZZAROLI, p. 10, fig. 5.

1992 Pseudodama farnetensis sp. nov.: AZZAROLI, p. 19, fig. 10, Pl. 5, fig. 2, a-b

1998 Euraxis eurygonos (AZZAROLI): DI STEFANO & PETRONIO, p. 53.

2001 Dama eurygonos (AZZAROLI): CROITOR, p. 98. 2003 Axis eurygonos (AZZAROLI): GIROTTI et al., p. 88

Original citation:

AZZAROLI (1947) introduced the subspecies *Dama nestii eurygonos* followed by a description and a figure of type specimen. The formal diagnosis was not proposed. The recent publication of AZZAROLI (1992) ignores the name "*eurygonos*".

Diagnosis:

The species is some-what larger than actual D. dama. The braincase is short, domed and flexed. The orbito-frontal region of skull is shortened. The anterior edge of orbit reaches the level of M². Orbits are relatively large. Pedicels are short and incranial. Frontal and parietal bones are convex. Unlike D. dama, the posterior edge of nasal bones does not reach behind the line connecting the anterior edges of eye sockets. The ascending part of mandible has more vertical position if compared to C. nestii. The angle between labial and lingual sides of molars is comparatively oblique and amounts to 37A. P_4 is molarized. Antlers are four-pointed, robust, widely spanned. The basal tine is situated at a little distance from the burr and forms with the antler beam an oblique angle. The distal fork is oriented in the parasagital plane. Metapodial bones are long. The metacarpus is longer than radius or almost of the same length.

Holotype:

The pair of antlers with pedicels and frontal bones IGF 245, MGUF.

Type locality:

Tasso, Upper Valdarno (Central Italy).

Description of holotype.

The type specimen IGF 245 is a fine frontlet with almost complete antlers (Fig. 13A). The distal portion o left antler was reconstructed later. The specimen displays a particular morphology of pedicels, which are remarkably short and incranial (Fig. 2). The antlers are comparatively robust,

four-pointed. The angle of divergence between first segments of antler beam s amounts to 95°. The second segments of beams are gently curved upright. The antler surface is pearled and sculptured with longitudinal ribs and furrows. The first time is strong and branches off at a very open angle close to the burr. The second time is small. The first and second segments of antler beam are almost of equal length, so the second time is in more proximal position if compared to *Cervus nestii*. Two massive long times compose the terminal bifurcation situated in the parasagittal plane. The anterior time is longer and forms a continuation of the beam, while the second time is implanted on the posterior side of the beam.

The antlers from Upper Valdarno.

AZZAROLI (1992) described the antlered frontlet IGF 356 as an abnormal specimen of *Pseudodama nestii* as the second (trez) tine is not developed (Fig. 13C). The short and robust incranial pedicels, the strong divergent beams with longitudinal ribs and furrows resemble the holotype of *Dama eurygonos*. The angle of antler divergence is about 115°. The left antler preserved a lateral flattening preceding



Fig. 13. *Dama eurygonos* AZZAROLI 1947: A, the fully grown pair of antlers IGF245 from Upper Valdarno, the holotype of species, oblique view (adapted from AZZAROLI, 1992); B, the antlered frontlet IGF 194v from Farneta, the type specimen of *D. eurygonos farnetensis* AZZAROLI 1992, oblique view; C, the juvenile specimen IGF 356 from Upper Valdarno, oblique view.

the oriented in the parasagittal plane distal fork. The basal tine springs off very close to the burr. The specimen IGF 356 is very interesting and, apparently, belongs to a juvenile individual and presents an early stage of ontogenetical development of antlers (see next chapter).

The skull IGF 244 from Tasso. (Fig. 8B, Fig. 14)

Antlers

Only basal fragments of antlers are preserved, as well as the proximal portion of beam of the left antler. The beam is curved sideward and is covered with longitudinal deep furrows and ridges. The basal tines spring off very close to the burr.

Skull

The skull is crushed in the dorso-ventral direction. The rostrum and the occipital part of the skull are destroyed. The braincase is very short, high-domed and flexed. Eye sockets are very large; the anterior edge of eye sockets reaches the level of the posterior edge of M^2 . The preorbital fossae are very large and deep with sharply outlined edges. The length of preorbital fossae is 33 mm (*sin*) and 30.5 mm (*dext*). Pedicels are incranial and short, slightly compressed in the latero-medial direction. Nasal bones are destroyed; however one can note that the posterior edge of *nasalia* is not



Fig. 14. *Dama eurygonos* AZZAROLI 1947 from Tasso: the frontal view of skull IGF 244, Upper Valdarno.

extended behind the line connecting the anterior edges of orbits. This character distinguishes *D. eurygonos* from *D. dama*.

Dentition

The specimen IGF 244 has preserved right M^2 and M^3 and left M^1 , M^2 and M^3 . The molars are deeply worn and some morphological details can not be observed. The angle between lingual and labial sides of upper molars amounts to 37A. The weak interrupted cingulum borders lingual sides of all molars, however it is somewhat stronger in M^1 .

The Lower Mandible IGF 242 from Figline.

The diastemal portion and processus angularis are destroyed. The dental part is very low and gently curved. The position of ascending part of mandible is more vertical if compared to the mandible IGF 243 of C. nestii. The upright position of the ascending portion of mandible is correlated with shortened face. The length of lower tooth row amounts to 91.0 mm. The height of horizontal part of mandible measured under M₁ amounts to 23.0 mm. The height of craniomandibular articulation surface is 80 mm. The lower premolar series amounts to 62.6% of the molar series length. Lower molars are supplemented with small ectostylides. The P_4 is molarised. The metaconide is extended toward the anterior and posterior; its anterior wing is merged with parastylide closing the anterior valley. The paraconide is not developed. The entoconide gets in touch with the entostilide and closes the posterior valley.

The articulated limbs.

Forelimbs (Tab. 3)

The specimen IGF 397 (*sin*) consists of the articulated distal fragment of *humerus*, *radius*, *os carpi radiale*, *os carpale secundum/tertium*, *metacarpus*, one *phalanx proximalis* and the both *phalanx media* (AZZAROLI, 1992: Pl. 9, Fig. 3). The proximal epiphysis of radius is narrowed if compared to *C. nestii*. The area of medial portion of the proximal articulation surface of radius is diminished if compared to *C. nestii*, while the *epicondylus lateralis* is stronger (Fig. 10). The incision for articulation with *processus coronoideus* of ulna is very shallow.

The metacarpus is almost of the same length as radius (the metacarpus/radius length index amounts to 98.6 %). The distal epiphysis of metacarpus is not broadened as sharp as in *C*. *nestii*. The distal part of the bone shaft is comparatively broad and compressed dorso-ventrally (Fig. 10).

Hindlimbs (Tab. 4)

The posterior limbs IGF 399 specimen includes articulated *talus*, *cubonaviculare*, *metatarsus* and phalanxes (AZ-ZAROLI, 1992: Pl. 9, Fig. 5). The metatarsal bone is long, its proximal epiphysis is narrow and deep (Fig. 11). Proximal phalanxes are weak and short if compared to *C. nestii*. Dama eurygonos eurygonos AZZAROLI 1947

Definition:

The antler section between the brow tine and trez (second) tine is not horizontal. The *metacarpus* is almost of the same length as *radius*.

Distribution:

Tasso Faunal Unit, late Villafranchian, Early Pleistocene (Italy).

Dama eurygonos farnetensis (AZZAROLI, 1992)

Original citation:

The species name *Pseudodama farnetensis* was originally proposed by AZZAROLI (1992: p. 19, Fig. 10) to designate an a d v a n ced representative of the genus *Pseudodama* AZZAROLI. The original description is supplemented by a formal definition and a figure of holotype.

Emended definition:

The antlers are large, robust, with strongly divergent beams, becoming horizontal is the section between the brow tine and trez (middle) tine. Metapodial bones are relatively long. *Metacarpus* is longer than *radius*.

Holotype.

A frontal fragment of skull with a pair of antlers IGF 194v (Farneta, Val di Chiana, Central Italy).

Distribution:

Farneta Faunal Unit, the latest Villafranchian, Early Pleistocene (Italy) (AZZAROLI, 1992).

Description of holotype.

The type specimen is characterised by the oblique angle of the basal bifurcation (about 155°) and strongly divergent beams, which become horizontal in a section below the trez tine (Fig. 13B). The right antler has a small middle tine, some-what shorter if compared to the type of D. eurygonos from Upper Valdarno. The middle tine of left antler is underdeveloped and is presented by a primordial tip. The distal bifurcation is made of two large tines compressed laterally and oriented in the parasagital plane. The frontal bones are convex. The pedicels are short, incranial, with almost circular transversal crosssection. However, the pedicles are slightly longer than in other specimens of Villafranchian fallow deer, including the holotype of D. eurygonos eurygonos, but they are still shorter if compared to the mature individuals of C. nestii (Fig. 2, Tab. 1). The length of pedicels suggests that the antlers from Farneta belong to a rather young individual. The rudimentary

second tines should be referred to the account of young individual age.

Additional material from Val di Chiana.

DE GIULI (1986) reported as "*Dama*" *cf. nestii* numerous fossil remains from Selvella, Val di Chiana. Later, AZZAROLI (1992) ascribed the fossils from Selvella to *Pseu* - *dodama farnetensis*. The sample from Selvella is of particular interest as it allows to associate together the postcranial elements and antlers of *D. eurygonos*.

The antlers are characterised by a very long and robust first tine implanted at a certain distance from the burr (DE GIULI, 1986: Pl. 8, Fig.1). The proximal portion of first tine is directed forward, and then the tine is turned upright. The apical part is pointed toward the posterior. DE GIULI (1986) noted the advanced molarisation of P_4 as well as the relatively short lower premolar series. Upper molars have weak trace of cingulum. The angle measured between labial and lingual slopes of upper molars amounts to 37°. The metacarpal bones are longer if compared to *D. eurygonos* from Upper Valdarno. The mean length of radius (n=3) amounts to 221.7 mm; the mean length of metacarpus of metacarpus and radius (the mean values) amounts to 101.0 %.

The distinguishing morphological characters between *D*. *e. farnetensis* from Val di Chiana and *D. eurygonos* from Upper Valdarno concern the minor differences in limb proportions, body size and antler beam curvature. Hence it is reasonable to keep *D. e. farnetensis* as an advanced subspecies of *D. eurygonos*.

Ontogenetic variation of antlers.

The various ontogenetic stages of antler development in D. eurygonos are represented by the sample from Selvella (DE GIULI, 1986). The pricket antlers are very little divergent with scattered pearling instead of the burr. The second year stage is presented by a two-pointed antler with a very long straight beam and a short basal tine. The angle of basal ramification is acute. The basal tine of young individuals is short and little curved. The antlered skull IGF 356 from Upper Valdarno presents the next stage of antler development characterised by strongly divergent antlers, the very well developed basal tine and the distal bifurcation, while the middle tine is still not developed (Fig. 13C). AZZAROLI (1992) regarded this antler as an aberrant individual. A little more advanced stage of development characterises the antlered skull IGF 194v with a primordial tip instead the middle tine on the left antler (Fig. 13B). The fully grown antlers have four tines. Unlike D. eurygonos, the antler development of the actual fallow deer D. dama is more accelerated. The second-year antler of D. dama already presents a morphological stage similar to the fully grown four-tined antler of D. eurygonos with the basal tine, the middle tine and the distal fork or even the small distal palmation (HUSAK, 1986).

Dama vallonnetensis (DE LUMLEY, KAHLKE, MOIGNE & MOULLÉ, 1988)

Synonymy:

1979 Dama nestii eurygonos AZZAROLI: PETRONIO, p.107, fig. 2. 1988 "Cervus" (s. l.) nestii vallonnetensis n. ssp.: DE LUMLEY et al., p. 483, fig. 14.

1998 Pseudodama nestii vallonnetensis (KAHLKE) : MOULLÉ, p. 34, fig. 2.

2001 Dama vallonnetensis (DE LUMLEY et al.): CROITOR, p. 99

Original citation:

DE LUMLEY *et al.* (1963) described a mandible with primitive P_4 of a smaller-sized deer from Vallonnet (South France) as *Cervus philisi* (DE LUMLEY *et al.*, 1963: p. 11, Fig. 2). Later, all the remains of smaller deer from Vallonnet and some finds from Untermassfeld (Germany) were ascribed to a new subspecies "*Cervus*" *s.l. nestii vallonnetensis* (DE LUMLEY *et al.*, 1988).

Emended definition.

The species is slightly larger than actual *D. dama*. Antlers are three-pointed, long and robust. First bifurcation is characterised by a very oblique angle. The first tine is strong, robust and rested on the burr. The second (middle, trez) tine is reduced. Two very long tines oriented in the parasagittal plane form the terminal fork. The anterior distal tine is a continuation of the beam; the posterior distal tine springs off on the posterior side of the beam. Pedicels are short with an incranial position. The braincase is flexed, domed and short, the eye sockets are large, the orbitofrontal part of skull is short.

Holotype:

A basal fragment of left (not right, as indicated in the original description) shed antler Nr. 10170, MPRM (DE LUMLEY *et al.*, 1988: p. 179, Fig. 14).

Type locality:

Vallonnet (Roquebrune-Cap-Martin, Alpes Maritimes, France).

Distribution.

Early Pleistocene, Latest Villafranchian – Postvillafranchian, Southern France, Italy.

Description of holotype.

DE LUMLEY *et al.* (1988) published the following brief description: "la ramure du petit cerf du Vallonnet se caractérise par un fort andouiller basal dont le diamètre

atteint celui du merrain et qui part au niveau de la rose. Toutes les ramures présentent cette même construction singulière, où l'extrémité de l'andouiller basal est très fortement recourbée vers la perche". It is necessary to add that the antler beam is set obliquely with respect to the burr and is directed backward and sideward. The antler surface is sculptured with longitudinal ridges and furrows, which are still observable on the eroded surface of the specimen. The difference between the type specimens of *D. vallonnetensis* and *D. eurygonos* concerns the position of the basal tine, which rests directly on the burr in the former species and is mounted at a certain distance from burr in the latter.

Additional material from Vallonnet.

The sample from Vallonnet consists mainly of isolated teeth, fragments of mandibles and several antler fragments. The revision of material revealed the presence of two deer species, a fallow deer D. vallonnetensis with rather advanced tooth morphology and another small-sized cervid of Axis type with primitive dentition, which will be discussed below. The remains of fallow deer are more numerous. Here will be considered only few remains to illustrate the diagnostic characters in the dental morphology.

Upper right molar M³ Nr. 1174 (MPRM), shows a comparatively advanced morphology. It is characterised by a moderately oblique lingual side that forms with the labial surface of tooth an angle of 37°. The additional enamel folds are not developed. The cingulum is not developed as well.

The fragment of left lower hemimandible Nr. 7879 (MPRM) maintains a complete tooth row. The P_4 is molarised with connection between metaconide and paraconide. The tooth row length amounts to 94.5 mm, the premolar series length amounts to 36.3 mm, the molar series length makes 58.6 mm. The premolar series amounts 61.9 % of the molar series length that is similar to the lower dentition proportion of *D. eurygonos* from Upper Valdarno. The premolar series of the fallow deer from Vallonnet is relatively some-what longer if compared to *D. clactoniana* from Riano, Italy (58.3%) and is close to the upper limits of the actual *D. dama* (46.0-61.6 %).

Dama vallonnetensis from Capena (Italy)

PETRONIO (1979) reported as *Dama nestii eurygonos* an almost complete male skeleton MPUR/M 988 and another antlered skull MPUR/M 1000 from the late Villafranchian site Capena (Rome). The skeleton with a complete pair of antlers belongs to a mature individual with fully developed dentition. PETRONIO (1979) noted the affinity of the antlers from Capena with *Dama nestii eurygonos* from Upper Valdarno. A single difference is the missing middle (trez) tine in antlers of the deer from Capena. The antlers are very robust, with a very long, strong and low situated basal tine and a distal bifurcation formed by two long tines oriented in the parasagital plane. The basal ramification is very oblique

and amounts to 135A (Fig. 15D). The length of terminal tines amounts to three quarters of the beam length measured between basal branch and distal bifurcation. Among the cranial characters of the deer from Capena, PETRONIO (1979) mentioned the short and incranial pedicels, relatively large orbits and short diastema correlated with shortened muzzle. The skull MPUR/M 1000 (PETRONIO, 1979: p. 107, Fig. 4) shows also a very short orbito-frontal part, rather short and flexed braincase that suggest the deer under discussion as a representative of the genus Dama. The shape of mandible with well developed processus angularis is very similar to the actual fallow deer. The morphology of P_4 is advanced: the anterior wing of metaconid is connected to paraconid. Metaconid is not extended toward the posterior (PETRONIO, 1979: p. 112, Fig. 14). The fallow deer from Capena isascribed here to Dama vallonnetensis due to its strong basal antler tine resting on the burr, the very obtuse angle of first ramification and short incranial pedicles.



Fig. 15. Antlers of early Pleistocene fallow deer: A, *Dama dama* L. 1758 (adapted from Husak, 1986); B, *Dama mesopotamica* BROOKE 1875 (adapted from Husak, 1986); C, *Dama eurygonos* AZZAROLI 1947 from Upper Valdarno (adapted from AZZAROLI, 1992); D, *Dama vallonnetensis* (DE LUMLEY *et al.*, 1988) from Capena, Italy (adapted from PETRONIO, 1979).

Dama vallonnetensis from Untermassfeld (Germany)

H.-D. KAHLKE (1997, 2001) described the abundant remains of *D. vallonnetensis* from the terminal Villafranchian site of Untermassfeld (Germany). The fallow deer from Untermassfeld is similar in size to *D. vallonnetensis* from Vallonnet and *D. eurygonos* and shows a broad range of size variation from *D. clactoniana* to the actual *D. dama* (Fig. 16). The lower premolar series is relatively short as in the advanced representatives of the genus *D. dama* and *D. clactoniana*. The antlers from Untermassfeld are similar to the deer from Capena. The massive basal tine rests on the burr and forms a very obtuse basal ramification. The middle tine is missing, while two strong crown tines form the distal ramification oriented in the parasagital plane (KAHLKE, 2001: tab. 75, Fig. 3, and tab. 76). Two fragmented antlers



Fig. 16. Proportions and length of lower tooth row of fossil and ectual fallow deer.

from Untermassfeld referred earlier to "C." nestii vallonnetensis (DE LUMLEY et al., 1988: p. 480, Fig. 15) rather belong to an Eucladoceros of ctenoides type (the fragment of shed antler) and to Metacervoceros rhenanus (the antler inserted in pedicle).

Dama cf. vallonnetensis from Pirro Nord (Italy)

A deer of similar type was reported from the Pirro Nord fauna (latest Villafranchian) of South Italy, as "Dama" cf. nestii (DE GIULI et al., 1986). The basal fragment of antler (Fig. 15D) is characterized by a basal tine inserted right above the burr, strongly curved upwards and forming an obtuse angle with the beam. DE GIULI et al. (1986) stressed a relatively short lower premolar row and regarded the deer from Pirro Nord as an advanced form of "Dama nestii". The deer from Pirro Nord is said to be the smallest form among the early Pleistocene fallow deer. Its size is close to the lower limit of the size variation range of D. vallonnetensis from Untermassfeld. The lower dentition size and proportions of the deer from Pirro Nord are similar to the actual fallow deer. The lower premolar series of the deer from Pirro Nord is relatively shorter than in D. eurygonos from Upper Valdarno and D. vallonnetensis from Vallonnet, but still falls within the variation range of D. vallonnetensis from Untermassfeld (Fig. 16).

Dama sp. from Ceyssaguet (Haute Loire), France

Among the very reach cervid fossils from Ceyssaguet (the latest Villafranchian), only a right upper jaw with P³-M³ (Cey-2-11010) and a left radiocubitus (Cey-2-10942) were ascribed to *Dama* (CROITOR & BONIFAY, 2001). The upper molars are characterized by a rather advanced morphology missing the spur of hypocone and the additional enamel folds of protocone. The angle between the lingual and labial sides of molars amounts to 35°. The length of upper molars suggests that the fallow deer from Ceyssagues is the smallest form among the fossil fallow deer from Western

Mediterranean (Tab. 5). However, the radius from Ceyssaguet is longer (202.0 mm) if compared to *D. cf.*

 TABLE 5

 The length of upper molar series in Villafranchian fallow deer.

Species	Site and source	M ¹ -M ² length (mm)
Дана гр.	Coysiagnet (CROTTOR & BONIFAY, 2001)	44,6
Dama of, vallannetensta	Piero Nord, MCUF	49,8
Dama surygonos	Selvella, G189, MGUF	52,6
Dama vallonneterste	Capena (PETRONID, 1979)	53,0; 54,6
Dama vallonnetensis	Untermanfeld (KARLEE, 1997)	51-53,5 (r=8)

vallonnetensis from Pirro Nord (182.6-191.1 mm).

Dama sp. from Slobozia Mare, Moldova

The basal fragment of left shed antler Nr. 26/20 (IZM) is the first evidence of presence of a fallow deer in the Villafranchian of Eastern Europe (Fig. 17). The specimen was collected from the upper part of the middle level of outcrops of Prut River near Slobozia Mare (South Moldova). The age of find most probably corresponds to the Middle or early Late Villafranchian. The basal tine of antler springs off at a little distance from the burr and forms a very obtuse angle (125°) with beam. The basal tine attains 180 mm of length and is quite weak and short if compared to *D. eurygonos* and *D. vallonnetensis*. The height of basal ramification amounts to 54.1 mm; the latero-medial diameter of antler above the burr amounts to 43.0 mm. The circumference of antler above the burr amounts to 138 mm.

Phylogeny of the genus Dama

The Villafranchian fallow deer show a strong affinity in cranial morphology with actual Dama dama. The Villafranchian and Modern species share the similar incranial position of short pedicles, the short, flexed and rounded braincase, the large orbits and the short face. Unlike fossil fallow deer, the antlers of D. dama are terminated by large palmation with digitations on the posterior side that look as merged crown tines (Fig. 15A). The ontogenetic development of antlers in D. dama is accelerated. D. dama shows the most advanced cranial characters among the fallow deer species, such as the strongest extension of nasal bones toward the posterior and the short contact between nasal and premaxillary bones. The actual fallow deer from the Middle East D. mesopotamica BROOKE possess several rather short crown tines implanted on the posterior side of the beam that occasionally may form a small palmation and a very large middle tine associated with additional prongs (Fig. 15B). The Villafranchian fallow deer like D. eurygonos has a rather weak middle tine and a single crown tine inserted on the posterior side of the beam (Fig. 15C). Nonetheless, the general plane of antler construction remains similar in all



Fig. 17. *Dama sp.* from Slobodzea Mare, Moldova: A, the medial view of shed right antler Nr. 26/20 (IZM); B, the basal view of antler.

fallow deer that includes the basal (brow) tine, the middle tine and the crown tines with posterior insertion on the beam. The evolution of antlers in the lineage D. eurygonos -D. vallonnetensis went toward the simplification with loss of the middle tine (Fig. 15D). In contrast, the Middle and late Pleistocene forms D. clactoniana FALCONER, D. carburangelensis DE GREGORIO, D. mesopotamica BROOKE and D. dama possess the many-tined and palmed antlers (LEONARDI & PETRONIO, 1976; DI STEFANO & PETRONIO, 1997; ABBAZZI et a l., 2001). According to DI STEFANO (1996), D. clactoniana and D. mesopotamica present a single phyletic lineage. The phylogenetic relationships between the Villafranchian fallow deer and the middle Pleistocene and actual species of are not clear yet. One can assume that a forerunner of the *eurygonos* type gave three parallel lineages: the lineage of the D. vallonnetensis in Western Europe, the clactoniana-mesoponamica lineage in the Near East and the stock of the modern European fallow deer with fossil subspecies Dama dama geiselana PFEIFFER 1998 and Dama dama tiberina DI STEFANO & PETRONIO 1997.

GEIST (1998) expressed a curious opinion on a possible phylogenetic relationship between *Megaloceros* and *Dama*. Actually, beside the palmed antlers, *Megaloceros giganteus* (650 kg) shares with actual *D. dama* (67 kg) some cranial characters as the caudal extension of nasal bones and relatively short face. Such a cranial proportion with relatively short face and long braincase is a primitive condition in deer (VISLOBOKOVA, 1990). However, this resemblance in cranial proportions between *M. giganteus* and *D. dama* seems to be superficial if *D. clactoniana* is involved in the comparison (Fig. 4). The latter species with the estimated body mass 140 kg has an advanced proportion of skull with very long muzzle. In this context, the giant deer has too "paedomorphic" skull proportions and does not fit with the "status" of giant fallow deer.

PIDOPLICZKO & FLEROW (1952) reported from Eastern Europe an obscure Pliocene deer suggested as an ancient relative of fallow deer. The new species Cervus (Cervodama) pontoborealis PIDOPLICZKO & FLEROW 1952 was established for a shed partially destroyed antler (Fig. 18) discovered near Mariupolis (former Zhdanov, Ukraine). The evidences supporting the Pliocene age of the find from Mariupolis were not provided. The antler belongs to a rather large deer (the maximal diameter of burr amounts to 56 mm) and presents a very short beam and a broad palmation ending by several long tines. PIDOPLICZKO & FLEROW (1952) assumed that the deer from Mariupolis is close to the actual Dama mesopotamica and included both species in the subgenus Cervodama. C. (Cervodama) pontoborealis was designated as a type species of Cervodama. The only single specimen, the hol otype of C. (Cervodama) pontoborealis, is known so far. KOROTKEVICZ (1970) and VISLOBOKOVA (1990) noted that the antler from Mariupolis is quite similar to the palmed antlers of Alces alces. However, they did not make a definite conclusion. In my opinion, the strong affinity of C. pontoborealis antler with A. alces is obvious. The unusually long tines in the antler from Mariupolis may be regarded as a hypertrophy, which is a common phenomenon in the late Quaternary deer. The belonging of shed antler described by PIDOPLICZKO & FLEROW (1952) to a late Pleistocene elk is the most probable. Hereby the species name C. (Cervodama) pontoborealis should be considered as a synonym of Alces alces L.

Ecology of Villafranchian Fallow deer

Unlike C. nestii, D. eurygonos has comparatively long metapodials and short slender phalanxes. The distal metapodial articulations are high and narrow, with narrow intertrochlean incision. The proximal epiphysis of first phalanx has a rather deep incision for the articulation with metapodial verticulus. These characters are interpreted by SOKOLOV et al. (1964) and KÖHLER (1993) as adaptations to open and dry habitats. The robust and widely spanned antlers and the advanced molarisation of short premolars supports the conclusion that D. eurygonos is an adapted to dry open landscape ecotype. The progressing adaptation to dry open lowlands explains the evolutionary changes in the lineage D. eurygonos – D. e. farnetensis – D. vallonnetensis, such as the gradual lengthening of the metapodial bones and the simplification of antlers. The metacarpus has almost the same length as the radius in D. eurygonos, while the metacarpal bone is longer than the radius in more advanced D. e. farnetensis. The longest metapodial bones are recorded in the middle Pleistocene D. clactoniana. The limb proportion change can not be correlated with the body size increase in the studied case. GAMBARYAN (1972) reported a correlation between the larger body size and the short distal segments of appendicular skeleton. The study of individual variation of the modern D. dama revealed the similar correlation, as the smaller individuals (mainly females) have the longer metapodials. The limb proportions (short humerus, long metapodials and particularly long metacarpus) of the Villafranchian *Dama* and the middle Pleistocene *D. clactoniana* are similar to the proportions reported by SOKOLOV *et al.* (1964) for *Gazella subgutturosa* inhabiting the open dry shrublands of Central Asia.

The loss of antler trez tine is the most peculiar evolutionary change of the lineage eurygonosvallonnetensis. This tine is quite weak in D. eurygonos and occurs only in fully-grown antlers of adult individuals. D. vallonnetensis completely lost this tine and is characterized by the three-pointed antlers for a second time. Probably, the trez tine in D. eurygonos has had the function of a hook fixing antlers of a rival in order to prevent the wounding during the males' combat. The loss of trez tine could be a consequence of the change in rutting behaviour of ancient fallow deer and the change of the antler function. The simplified, but comparatively large antlers of D. vallonnetensis could serve the function of social display and their effective weapon function was insignificant. The simplified antlers of D. eurygonos do not contradict to the possible adaptation in the open landscape. In opinion of CARO et al. (2003), there is no association between manytined antlers of deer and open environment.

Genus Metacervoceros DIETRICH 1938

Definition.

The braincase is long and unflexed. The pedicels are long and sloped backward. The orbitofrontal region is short; the anterior edge of eye sockets reaches the level of M^2 . The size of orbits is normal. The bulla timpani are large and rounded. The basioccipital bone is broadened. Upper molars has well-developed or rudimentary cingulum. The lingual wall of upper molars is very oblique. The angle between lingual and labial walls of upper molars is wider than 40°. Upper canines are not developed. Lower molars have no *Paleomeryx* fold. The morphology of P₄ is simple. The first tine is always situated at a rather long distance from the burr. The basal tine and the distal fork are oriented in the same plane.

Type species:

Cervus pardinensis CROIZET & JOBERT 1828

Other referred species:

M. rhenanus (DUBOIS, 1904), *Metacervoceros warthae* (CZYZEWSKA, 1968)

Distribution.

Late Pliocene – Early Pleistocene, Villafranchian, Europe.

Metacervoceros rhenanus (DUBOIS, 1904)

Synonymy:

1904 Cervus (Axis) rhenanus sp. nov.: DUBOIS, p. 219, fig. 2

1941 Cervus philisi sp. nov.: SCHAUB, p. 264, pl. 17

1952 «Cervus» perolensis sp. nov.: BOUT & AZZAROLI, p. 51, fig. 8

1990 Cervus (Rusa) philisi (SCHAUB): VISLOBOKOVA, p. 154

1990 Cervus (Rusa) perolensis (AZZAROLI): VISLOBOKOVA, p. 154

1992 Pseudodama rhenanus (DUBOIS): AZZAROLI, p. 4

1992 Pseudodama perolensis (AZZAROLI): AZZAROLI, p. 4

1992 *Pseudodama* cf. *lyra* (AZZAROLI) (*partim*): AZZAROLI,: pl. 3, fig. 1 a-b.

1992 Cervus ichnoceros sp. nov.: BOEUF et al., p. 166, pl. III, fig. a, 1-2

1992 Cervus rhenanus (DUBOIS): SPAAN, p. 23, fig. 8

1997 Dama (Pseudodama) rhenanus (DUBOIS): PFEIFFER, p. 38

2001 *Metacervoceros rhenanus* (DUBOIS): CROITOR & BONIFAY, p. 138, figs. 13-17

Original citation:

DUBOIS (1904) introduced the species name *Cervus* (*Axis*) *rhenanus* for a small-sized deer from Tegelen. The original species name citation is accompanied by a figure of the type specimen but not by any description.

Species revision:

SPAAN (1992) carried out a detailed revision of the original material from the type locality and species and arrived to a conclusion on the synonymy of *Cervus rhenanus* from Tegelen and *Cervus philisi* from Senèze. The revision is based on the antler and dentition morphology and lacks the study of cranial morphology. CROITOR & BONIFAY (2001) included the species under study in the genus *Meta - cervoceros* DIETRICH 1938 with type species *C. pardinensis* CROIZET & JOBERT.

Holotype:

The unshed complete left antler Ha 15777 is the holotype of species. The detailed description of the holotype was recently published by SPAAN (1992: Fig. 8).

Emended definition:

The size of species is similar or slightly larger than actual *Axis axis*. The antlers are three-pointed. The basal tine is situated at a certain distance from the burr. The angle of first ramification vary from 100° to 60° . The distal bifurcation is situated in the same plane as the basal tine. The posterior tine of distal fork is longer than the anterior one. The pedicles are long and pointed toward the posterior. The braincase is rather long, unflexed, with slightly convex parietal bones. The suture between nasal and premaxillar

bones is long. The anterior part of each frontal bone is slightly swollen. The preorbital fossae and ethmoidal openings are large. The size of entostyle is variable; a weak cingulum may be present in upper molars. Upper canines are not developed. The lower fourth premolar is primitive. The *processus angularis* is well-expressed. The diastema of lower mandible is slightly longer than lower molar series.

M. rhenanus from Senèze

The female skull Nr. 210638 (PMUL).

The specimen is almost complete with exception of the destroyed left premaxillar bone. The braincase is slightly damaged and deformed. The profile of frontal bones is concave at the level of the anterior half of orbits (Fig. 1°C). The anterior part of each frontal bone is slightly swollen. The nasal bones are extended behind the line connecting the anterior edges of the orbits (Fig. 20). The preorbital fossae are well developed and deep. The ethmoidal openings are very large with a rather long border (18 mm) with the nasal bones. Such a contact of the nasal bone with ethmoidal opening is longer than in *Cervus*, but shorter than in *Dama*. The suture between nasal and premalillar bone is long (23 mm) like in *Cervus*, and much longer if compared to the actual *D. dama*. The braincase is elongated, unflexed and not rounded as in *Dama*. The parietal bones are just slightly



Fig. 18. The holotype of *Cervus (Cervodama) pontoborealis* PIDO-PLICZKO & FLEROW 1952 (= *Alces alces* L). Adapted from PIDOPLIC-ZKO & FLEROW (1952).





Fig. 19. Cranial morphology of deer females: A, actual Dama dama (adapted from SOKOLOV, 1959); B, actual Cervus elaphus (adapted from SOKOLOV, 1959); C, Metacervoceros rhenanus (DUBOIS, 1904) from Seneze, Nr. 210638 (PMUL); D, the braincase outlines of Metacervoceros cf. rhenanus from Olivola, IGF 1403 (adapted from AZZAROLI, 1947).

convex. Bulla timpani are rounded, smooth, and moderately large with maximal diameter of 18.0 mm. Bulla timpani protrude a little below the basioccipital surface. The basioccipital bone is broad (Fig. 21). The face length measured from the anterior edge of orbits to prostion amounts to 56.9% of the condylobasal length and is relatively longer than in A. porcinus and C. nippon. The predental part is shorter than the length of upper tooth row. The general proportions of the skull are very close to females the actual Axis axis (Fig. 22, Tab. 6). Unlike the actual species of Axis, M. rhenanus shows a significantly shorter frontal suture with respect to the skull length (Fig. 23). Apparently, it is correlated with the stronger posterior extension of the nasal bones in M. rhenanus than in modern Axis.

Fig. 20. Metacervoceros rhenanus (DUBOIS, 1904) from Seneze: frontal view of the female skull Nr. 210638 (PMUL).



Fig. 21. Shape of basioccipitale: A, Dama dama; B, Cervus elaphus, C, Metacervoceros rhenanus, Nr. 210638 (PMUL). Not to scale

The male skull Nr. 210774 (PMUL).

The left side of the skull is badly damaged. The predental part of the skull is destroyed (Fig. 24, Tab. 7). The pedicles are rather long and set obliquely on the skull. The angle between pedicle and parietal bone amounts to 70°. The frontal bones are convex between the bases of pedicles. The

Roman Croitor



Fig. 22. Cranial proportions in fossil and actual deer (females): the relative length of face (%) measured from orbit to *prostion* with respect to the condylobasal length.

TABLE 6

The measurements of female crania of *Metacervoceros rhenanus* (DUBOIS, 1904) from Senèze and actual deer of the genus *Axis*.

· · · · ·	M chenanae	A. porcious	A ands
Measurements (nov.)	Nr. 210698, PMUL	206,7,59; NHML	1845.11.195, NEML
Contylobasal longfh	283.0	210.0	252.0
Length of upper tooth row P ² -M ²	88.0	65.6	77.0
Leogth of upper molars M'-M"	50,7	39.4	48.4
Leogth of upper premolars P2-P4	39.3	35.0	30.3
Distance P ² -provision (prodental length)	83.0	64. B	78.5
Distance M ³ - occipital condylas	189.3	B1.1	98.3
Oscipital width	73.0	72.8	79.6
Occipital height	62.8	49.3	53.7
Width of occipital condyles	51.8	39.8	46.2
Maximal width of barioceipitale	36.7	29.1	33,0
Face length (orbit - prortion)	161.0	110.5	142.0
Dismoter of eye society	45.0	33.7	38.5
Length of frontal summe	68.0	75.0	78.3
Distance brogma - opistocrasion	75.0	55.Z	70,4
	Jan 24		÷

skull profile is concave in front of the pedicles. The anterior part if each frontal bone is swollen. The relief of frontal bones is stronger expressed than in the female skull. The anterior edge of orbit is situated at the level of M^3 middle.

The hypocone and protocone of P^2 are separated. The hypocone of P^2 has an internal enamel fold. The lingual wall of P^3 has a vertical grove separating the merged hypocone and protocone. The hypocone of P^3 has an internal enamel fold as well. There is no separation of hypocone and protocone in P^4 . Upper molars are supplemented with entostyle. The additional enamel folds of protocone and hypocone are not developed. The angle measured between protocone and paracone external walls amounts to 42° . The cingulum is not developed in the specimen Nr. 210774. However, a weak continuous cingulum bordering the base of protocone is recorded in isolated molars from Senèze Nr. 210556, Nr. 210559 and Nr. 210557.

The lower mandible Nr. 209564 (PMUL).

The mandible (Fig. 25) is characterized by a rather long



Fig. 23. Cranial proportions in fossil and actual deer (females): the relative length of frontal suture and braincase (measured from *bregma* to *opistocranion*) with respect to the condylobasal length.



Fig. 24. *Metacervoceros rhenanus* (DUBOIS, 1904) from Seneze: oblique view of the male skull Nr. 210774 (PMUL).

 TABLE 7

 Metacervoceros rhenanus (DUBOIS, 1904): measurements of male skulls.

Maramana anda (anna)	Sman PMOL	Olivala MGUF	Coynagaet, MDC			Maatapali. MGUF
predeteration (usual	Nr. 210774	3C3F3404	2318	<u> </u>	11217	EF142EV
Length of upper tooth row P ² -M ²	85.1	85.2	87.2	83,8		84.8
Length of upper molans M1-M1	50.8	50.9	51,4	49.4		50.7
Laugh of upper premolers $\mathbf{P}^2 \cdot \mathbf{P}^4$	36.0	37.8	39.2	37.0		36.6
Distance M _occipital condyles		120.0				127.0
Occipital width	[102.3		(····	97.0	104.3
Occipital height		65.9			66.7	64.8
Prontal width	98.0	91.2	98,8	104.6	103.1	94.0
Width behind pedicles	72.5		82.8	82.2	77.7	
Width of occipital condyles		·			58,0	50.6
Maximal width of basicostpitals		37.0		†	41.1	37.0
Diameter of eye sockets	<u> </u>			42.6	· ·	-
Length of frontal soture		<u> </u>		B4.0		<u> </u>
Distance bregma - opintocranion	82.5	81.7		79.5	74.3	81.0
Pedicle length from arbit	64.6	· · ·	·····	-		

Meanacannia (con)	Coy-14760 dr	Coy-15179.cm	Cop-13194 dž	Coy-13194 air
Height of pedicle	23.0		23.3	22.7
Antero-posterior diameter of pedicle	23.6		29.7	30.8
Latero-medial diameter of pedials	22.3		29.9	30.6
Antero-posterior diameter above hurr	25.2	27.9	35.8	33.7
Latero-medial diameter above burr	19.8	19.0	38.5	35.5
Height of first ramification	41.6	45.8	83.5	62.1
Height of second multication	280.0	255.0	512.0	502.0
Length of first time	60.0	34.3	220.0	210.0
Length of second tine	30.0	[120.0	105.0
Length of third time			257.0	235.0
Length of second segment of beam	244.0	225.0	430.0	425.0
Total length of entire	306.0	280.0	785.0	736.0

TABLE 8 Metacervoceros rhenanus (DUBOIS, 1904) from Ceyssaguet: measurements of antlers.

diastema, which is slightly longer than the series of lower molars. It is comparatively longer than in *C. nestii*, *C. nippon* and *D. dama*, however, is shorter if compared to *A. porcinus* and *C. elaphus* (Fig. 7). The ratio between premolars and molars vary from 61.4 to 65.8% (n=7); the mean value of relative length of premolars amounts to 63.5%. The ascending part of mandible is slightly inclined toward the posterior. The *processus angularis* is strong. There is only one anterior ectostylide in M_3 that is quite weak if compared to ectostylides of M_2 and M_1 . The lower fourth premolar (P₄) is simple.

5 cm



Fig. 26. *Metacervoceros rhenanus* (DUBOIS, 1904) from Ceyssaguet: The antlered skull Cey-2318.



Fig. 27. *Metacervoceros rhenanus* (DUBOIS, 1904) from Ceyssaguet: the side view of skull Cey-2318.

Central French Massive)

M. rhenanus from Ceyssaguet (Haute-Loire,

The preliminary description of *M. rhenanus* from Ceyssaguet was published by CROITOR & BONIFAY (2001) and restricted to the study of diagnostic characters.

Fig. 25. Metacervoceros rhenanus (DUBOIS, 1904) from Seneze:

The antlered skull Cey-2-2318.

lower mandible Nr. 209564 (PMUL).

The braincase and predental part of the antlered skull CEY-2-2318 (MNP) are destroyed (Figs 26-28, Tab. 7).

Antlers

The antlers are three-pointed and lightly built. The total antler length in the skull CEY-2-2318 (Fig. 26) amounts to 760 mm (*dext*) and to 767 mm (*sin*). The distance between the antler base and the top in the same specimen amounts to 710 mm (*dext*) and to 732 mm (*sin*). The distance between tops of the antler amounts to 565 mm. The proximal parts of antler beams form an angle of 70°. The second third of antlers is



Fig. 28. *Metacervoceros rhenanus* (DUBOIS, 1904) from Ceyssaguet: the frontal view of skull Cey-2318.

bow-shaped and more divergent. The distal portions of antlers are more or less parallel each to another. The angle of first ramification amounts to 60°. The basal tine is situated at a certain distance from the burr. The distal bifurcation is oriented in the parasagittal plane and formed by the second tine inserted on the anterior side of the beam. The antler beam becomes compressed laterally in the area of the distal bifurcation. The antler surface may be depressed from the sides in the area of the bifurcation. The angle of distal bifurcation amounts approximately to 40-45A. The transversal section of antler tines is circular. The antler surface is pearled and sculptured with longitudinal ribs and furrows. The measurements of complete antlers from Ceyssaguet are quoted in the Tab. 8.

Skull

The long pedicles are slightly dorso-ventrally compressed and sloped backward from the face. The anterior edge of eye sockets reaches the level of M^2 (Fig. 27). Nasal bones are comparatively long and extend behind the line connecting the anterior edges of eye sockets (Fig. 28). The preorbital fossae are very large and deep. The ethmoidal openings are large. The border of ethmoidal opening formed by nasal bones is very short. The lateral profile of frontal suture is convex between pedicles and is depressed between the orbits. The anterior parts of both frontal bones are somewhat swollen showing a typical for *M. rhenanus* relief of forehead.

Upper Teeth

Upper molars have a weak trace of cingulum, protoconal fold and eperon. Their parastyles and mesostyles are well developed and prominent. The ribs on labial side of paracone and metacone are also well pronounced and sharp. The interior enamel of hypocone of upper premolars is folded.

The antiered skull Cey-2-11217.

A neural part of skull is preserved only in the specimen CEY-2-11217 (Fig. 29, Tab. 7). The terminal tines of the antlers are broken off. The braincase is long like in *Axis*, and much longer if compared to *Cervus* and *Dama*.



Fig. 29. *Metacervoceros rhenanus* (DUBOIS, 1904) from Ceyssaguet: the side view of skull Cey-11217.

Lower Mandible

The relative length of premolars is similar to the sample from Senèze (Tab. 9). The specimen Cey-2-5415 with a complete cheek tooth row belongs to a mature individual with slightly worn molars (Fig. 30). Lower molars lack the *Palaeo* - *meryx* fold, while the ectostylid is well developed in all molars. The moralisation of P_4 is quite primitive; however, sometimes the posterior lobe of metaconid is connected with entoconid.

The left hemimendible Cey-2-10851 belongs to a juvenile individual with deciduous teeth. The deciduous teeth are deeply worn, without the *Palaeomeryx* fold or any additional enamel folds. Dp₃ is supplemented with an anterior ectostylide. The crown of I₁ is very wide, triangle



Fig. 30. *Metacervoceros rhenanus* (DUBOIS, 1904) from Ceyssaguet: the lateral view of lower mandible Cey-5415 (*sin*) and occlusion view of lower tooth low.

TABLE 9 Metacervoceros rhenanus (DUBOIS, 1904): measurements of lower mandibles.

	Vall	1	Seneza		C	oy none me	1	Splochie
Measurements	416	210552	210565	310771	15118	\$415	14847	LOF 1471y
Length of tooth	89.1	190.1	96.1	95.0	84.8	98.1		86.7
20W Py-Ma								ļ
Longth of promotions P ₂ -P ₂	34.8	38.0	37.5	37.0	32.4	39,8	3B.4	33.8
Lough of noises M ₁ -M ₂	54.7	61,0	58.A	56.2	52.8	59.2		52.2
Length of Incritantial comes				220.0			,-	220.0
Longth of dissions Py-C		62.0	60.4	57.0			52.3	55.6
Distance between P ₂ and foremen		43.0			38.6	35.0	30.6	35.1
noniale Mandhia height under Pr		20.5	22.6	20.4	21.8	18.8	20.8	28.6
Mandibia beight under M ₁		26.6	24.5	26.0	25.3	25.3		27.7
Heigh of articulation				73.6				80.0
Beight of Meanding means				106.5				115.0
Premisiani molani Initia (%)	63.6	62.3	64.2	65.8	61.4	67.2		64.7

TABLE 10 Metacervoceros rhenanus (DUBOIS, 1904) from Ceyssaguet: measurements of articulated posterior limbs.

Skalatal elements and tilken measurements (mm)	m) Collection number and measurement	
Tibia		Cey-10373
Distel breadth		34.0
Distal depth		27.0
Cricanus	Cey-10502	· Cey-10271
Greatest length	\$6.6	64.9
Length of tubercle	60.5	58.5
Distal width of taburcle	20.7	19.3
Teles	Cey-10501	Cey-10265
Grostert length	41.0	39.6
Breadth of distal trochles.	25.7	24.6
Depth of distal truchlea	20.6	19.5
Catomericalare		Cep-10266
Groupst broadth		31.2
Greatest depth	ļ	26,5
Meinteren	Cay-16499	Cay-10265
Maximal length	234.0	
Breadth of proximal opiphysis	28.7	27.0
Depth of proximal epiphysis	31.B	30.0
Breacth of distal epiphysis	32.4	
Dismeter of distal articulations	21.7	· · ·

shaped, asymmetric with extended lateral angle. I_2 , I_3 and C are smaller and very narrow.

Articulated posterior limbs.

The measurements of postcranial remains are quoted in the Tab. 10. The length of calcaneus amounts to 37.0% of the metatarsus length. The calcaneus of M. rhenanus is rather short if compared to *C. nestii* and *C. elaphus*.

Articulated phalanges CEY-2/3-11305.

The proximal and medial phalanges are associated with a fragment of distal articular part of a metapodial bone. The distal metapodial articulation is rather high if compared to actual *Dama dama*. The verticillus is weak. The first phalanx is long, narrowed, slender and smooth, if compared to Villafranchian *Pseudodama nestii* and *Dama eur y g o n o s* from Italy. The second phalanx is relatively long if compared to Italian small-sized deer, with very weak plateau postarticulaire and narrowed epiphyses. The length of proximal phalange amounts to 48.5 mm, the breadth of proximal epiphysis amounts to 15.4 mm, the depth of epiphysis amounts to 19.7 mm. The corresponding measurements of middle phalange amount to 31.2 mm, 13.7 mm and 19.5 mm. The length of hoof phalange amounts to 35.7 mm.

M. rhenanus from Vallonnet

(Roquebrune-cap-martin, Alpes-maritimes, France)

The early report on fauna from Vallonnet mentions a lower mandible with primitive dentition of Cervus philisi (DE LUMLEY et al. 1963: p. 11, Fig. 2). The revision of material revealed some more dental remains that belong to a deer from much more primitive than Dama. The upper isolated molar M³ R12079 (MPRM) is characterised by a very oblique lingual side that forms with the labial surface of tooth an angle of 45° and a clear cingulum that borders the base of protocone. The posterior wing of protocone has an additional enamel fold. This combination of characters is found in several isolated teeth. To M. rhenanus belongs also the left hemimandible Nr. 416 with primitive P_4 . The mandible shows a great affinity in morphology, size and dental proportions with M. rhenanus from Ceyssaguet Tab. 9). The antler remains from Vallonnet are very scant and the specific determination in many cases is impossible.

M. rhenanus from Milcovu din Vale (Oltenia, Romania)

The braincase with pedicles of a small-sized deer from the upper Villafranchian deposits of Milcovu din Vale (Olt river valley) is stored in the Laboratory of Paleontology of the University of Bucharest. The deer was found in association with *Archidiskodon meridionalis* and *Paracamelus alutensis* (RADULESCU, personal communication). The braincase

behind pedicles is relatively long (84.0 mm). The breadth of braincase behind pedicles is 199.5 mm. The occipital breadth amounts to 199.5 mm. The breadth of occipital condyles amounts to 64.3 mm. The pedicles are long.

M. cf. rhenanus from Upper Valdarno (Cerntal Italy)

The skull IGF 1408 was ascribed by AZZAROLI to Pseudodama nestii (AZZAROLI, 1992: Pl. 3, Fig. 1 a-b). The specimen is badly crushed and its anterior part is destroyed. Only the right antler is present. The specimen belongs to a very old animal with a deeply worn dentition.

The first tine branches off very high from the burr forming an acute angle whith the beam (about 55°). The anteroposterior diameter of antler above the burr is 45.1 mm, the latero-medial diameter is 34.7 mm, and the height of first ramification is 59.4 mm. The pedicels are very long, sloped backward from the face. The transversal diameter of right pedicle is 38.1 mm; the pedicle length measured from the orbit to the burr is 63.8 mm. Although the skull is deformed, one can observe that the orbito-frontal region is rather short as the anterior edge of orbits almost reaches the level of M^2 . The cingulum is well developed in M³, it is quite weak in M² and completely reduced in M¹. The lingual and labial sides of the upper molars form an angle of 63°.

The left lower hemimandible IGF 1471v from Spicchio (Fig. 31; Tab. 9) was originally described as Pseudodama cf. lyra (AZZAROLI, 1992). The horizontal ramus is very deep and strong. The diastemal part is slightly longer than lower molar series (Fig. 7) and comparatively longer than in D. eurygonos and C. nestii. The ascending ramus is in vertical position, very high and relatively narrow. The angle between horizontal and ascending parts of mandible is 98°. The processus angularis is well developed and extended toward the posterior. The lower premolar series is relatively long (67.4 %). The morphology of P_4 is simple.

M. cf. rhenanus from Olivola (Central Italy)

AZZAROLI (1947) figured the lateral profile of skull IGF-



Fig. 31. Metacervoceros cf. rhenanus (DUBOIS, 1904) from Spicchio Fig. 32. Metacervoceros cf. rhenanus (DUBOIS, 1904) from Olivola (Italy): the lateral view of lower mandible IGF 1471v (sin).

1403 reported as an aberrant form of Dama nestii eurygonos (Fig. 19D) with particularly long braincase. The skull rather belongs to a deer very close or even identical to M. rhenanus from France. The skull is characterized by very long pedicles sloped backward from the face, large preorbital fossae, large ethmoidal openings with short border with nasal bone and a short orbitofrontal part (Fig. 32). However, unlike M. rhenanus from Senèze and Ceyssaguet, the deer from Olivola has short nasal bones that do not reach the line connecting the anterior edges of orbits. The short nasal bones are a primitive condition of character and suggest the deer from Olivola as a more archaic form similar to actual Axis. The cranial fragments figured by AZZAROLI (1947: p.52, Fig. 1; 1992: p. 15, Fig. 7) also should be ascribed to M. cf. rhenanus. Few remains from Olivola, like the fragment the so-called aberrant antler (AZZAROLI, 1947: p. 56, Fig. 5-3) probably, belong to Dama.

Individual variation of M. rhenanus

The cingulum in upper molars is a variable character. A weak continuous cingulum is recorded only in three specimens (all M^3) of the sample from Senèze. In the majority remains (22) specimens) the cingulum was interrupted or completely reduced. The cingulum seems to be more frequent in the sample from Vallonnet. The individual variation of P_4 is



(Italy): the frontal view of skull IGF1403.

studied in the sample from Ceyssaguet. The extended caudally metaconide of P_4 is merged in some cases with entoconide. The contact between metaconide and paraconide was not observed. What concerns the antler morphology, the angle of first ramification seems to be the most variable character.

The angle of basal bifurcation in the sample from Ceyssaguet varies from 60° in the skull CEY-2-2318 to 100A in the shed antler CEY2-10564. The height of first ramification varies in the sample from Ceyssaguet from 41.6 mm to 83.5 mm.

The cranial remains from Upper Valdarno and Olivola are characterised by such primitive characters as very oblique lingual wall of upper molars and short nasal bones and may represent a distinct form closely related to *M*. *rhenanus*.

Systematic position

DIETRICH (1938) created the subgenus Metacervoceros for fossil European Rusoid deer with primitive three-tined antlers. The Early Villafranchian species Cervus pardinensis CROIZET & JOBERT was selected as a type species. HEINTZ (1970) suggested the early Villafranchian Cervus s.l. pardinensis as a direct forerunner of C. philisi (=M. rhenanus). CROITOR & BONIFAY (2001) and CROITOR & STEFANIAK (in press) included in the genus Metacervoceros the species M. pardinensis (CROIZET & JOBERT), M. warthae (CZYZEWSKA) and M. rhenanus (DUBOIS). The cranial proportions of *M. rhenanus* and such morphological peculiarities as the long pedicles and rather large and rounded bulla timpani approach the deer under consideration to actual Axis. However unlike Axis, M. rhenanus shows such a derived character as long caudally extended nasal bones. M. cf. rhenanus from Olivola with short nasal bones shows a greater affinity with modern Axis deer. M. warthae from the late Pliocene of Eastern Europe is similar to M. rhenanus in dental morphology, shape and size of bulla timpani, the broadened shape of basioccipitale, position of pedicles and shape of frontal bones (CROITOR & STEFANIAK, in press). Unlike M. rhenanus, M. warthae was some-what larger with estimated body mass of 120 kg and possessed the more complicate antlers with small distal flattening terminated by three distal prongs.

Ecology of M. rhenanus

The feeding ecology of *M. rhenanus* also reminds modern grazing *Axis*. The mesowear analysis of *M. rhenanus* from Ceyssaguet revealed the pattern of tooth wearing similar to the tooth wearing of the modern African grazers *Redunca redunca* and *Kobus ellipsiprymnus* that live near rivers and feed on juicy fresh grass (CROITOR & KAISER, 2002; KAISER & CROITOR, in press). Actually, juicy but quite abrasive grass, which mostly is rich in phytoliths, seems to be readily available forage for the Ceyssaguet deer. Therefore, *M.*

rhenanus from Ceyssaguet are likely to have incorporated a considerable amount of grass in their diet that usually can be found in abundant quantity near a water body in the conditions of relatively cold climate (BONIFAY, pers. comm.). Unlike actual Axis, M. rhenanus from Ceyssaguet was exposed to a significant environmental seasonality that may be concluded from the broken tips of labial cusp apices of molars in some specimens. This type of damage of cusp tips is recorded quite often in M. rhenanus, both in upper and lower cheek teeth. The broken tooth tips were freshly damaged or slightly polished by food, a fact that suggests, that the tips were damaged during the animal's life shortly before its death. Apparently, during the winter season, the diet of M. rhenanus should have included higher proportions of rough and abrasive food components like dry grass, tree shoots and bark. This seasonal change in diet could have caused the observed damage of tooth tips with consequent polishing by abrasive material. The antlers preserved still attached to the pedicles suggest that M. rhenanus inhabited the area near the Ceyssaguet site during the winter season. Apparently, this small-sized deer inhabited dense woodland and areas with tall grass near the water (KAISER & CROITOR, in press).

DISCUSSION

The separation of phylogenetic stocks that lead to Dama and Cervus took place during the late Miocene 8.2-11.9 Ma ago (RANDI et al., 1998), thus the belonging of early Pleistocene small-sized deer of Europe to different genera can not raise doubts. The finds of the earliest true representatives of the genus Cervus are known so far only from Italy and Georgia. C. nestii belongs to the long-faced red deer group or the "elaphus" group and is characteristic of Tasso faunal Unit of Italy. D. eurygonos and D. vallonnetensis belong to a vanished group of primitive fallow deer with simple nonpalmed antlers. The distribution of Dama during early late Villafranchian ranged from Moldova to Italy. By the end of Villafranchian, the area of fallow deer distribution increased and included also Spain, France and Germany (CROITOR & BONIFAY, 2001; KAHLKE, 2001; CUENCA-BESCOS & GARSIA, 2004).

Apparently, the small-sized Early Pleistocene *Dama* and *Cervus* from Ponto-mediterranean area were ecologically and evolutionally flexible enough to resist the climate cataclysms of the Quaternary period and survived until the present days. Both genera gave rather successful middle Pleistocene large-sized forms *D. clactoniana* and *C. elaphus* that were characterized by the complicate antlers many-tined (*Cervus*) or palmed (*Dama*) antlers and the two times larger body size. The archaic forms like *Cervus elaphus barbarus* and *Dama mesopotamica* survived in the glacial refugia of Atlas in North Africa and the Middle East.

The ecological adaptations of small-sized deer from Upper Valdamo suggest that the forest dweller adapted to the mountainous landscape *C. nestii* and the open landscape

Roman Croitor

TABLE 11

The comparison of diagnostic characters of small-sized Villafranchian deer from Italy.

Matazar vocarar rhanana	Corves next	Дана соуд алоз
1. Bye sockets are of normal size,	1. Bye societs are small, their	1. Eye sociats are large, their
their animier edges reach the lavel	antarior algos de not reaches fac	enterior edges reach the level of
of \mathbf{M}^2 (the orbitalization is	level of M ² (the arbitrhystal	M ^a (the origination of
short).	partion in long).	skull is shart).
2. The the enterior part of each	2. Frants! and periots! bonce are	2. Presidul and parlatel borne are
ficatel bone is swellen.	fint.	CUTTING.
3. Need bance are extended	3. Nasal benes do not much the	3. Naml bones are extended
bahind the line connecting the	line connecting the enterior edges	behind the line connecting the
exterior edges of orbits.	of orbits.	abterior edges of orbits.
4. The offennidal openings are	4. The etimoidal openings are	4. The official openings are
contacted by meral bone at a	contacted by musil bons at a	other the part of the second second
distance shorter than 5 of the	distance shorter than 5 of the	distance longer than 6 of the
ethensidel langth.	ethionidal length.	otimoidal lengti.
5. The brainces is very long and	S. The braincase is rather long and	5. The bruthents is short and
unflexed.	mflened.	fittal
6. Pediocle are long and directed	6. Pedicels are long and directed	6. Pedloels are about and set
toward posterior.	towned pocketier.	increasially.
7. The angle between ascending	7. The angle between according	7. The angle between anothering
and borizontal portions of	and harizontal particus of	and horizontal portions of
mendible amounts to ~ 98°.	mendible amounts to ~109°.	mendible apidants to 102".
8. The diastents of mendible is	8. The diastems of mandible is	5. The discourse of mandfuls is
longer then lower make perios.	shorter or of the same length as	director than lower major series.
	lower motor series.	
9. Pels primitive.	9. P ₄ is primitive.	9. P. is molarised.
10. Cingulara in opper molars is	10. Cingulous in opper molars is	10. Clignitum is very network.
variable and weak.	not developed.	
11. The angle between lingual and	11. The angle between lingual and	11. The male between impul and
labilitation of upper molecular	labial aides of apper molars	labial sides of upper molars
larger than 40°.	amounts to 30".	pennende ta 37º.
12. Epiptyses of limb hungs are	12. Epiphyses of limb banes are	12. Bpiphyres of itmb bones are
comparatively wide.	comparatively wide.	contpanetively narrow.
13. Mempedials are long.	13. Metapodhin are short.	13. Metapodials are long.
	<u> </u>	

cursorial runner *D. eurygonos* were ecologically separated. Both the deer species are important back-ground elements of the Tasso Faunal Unit from Italy and suggest the mixed character of landscape with mountainous forests and more open and dry landscape of the savannah woodland type in the lowlands. The ecological diversity of species composing the Upper Valdarno fauna suggests that the taphocenosis formed on a watering place frequented by species from different ecosystems. The evolutionary trends in antler morphology and limb proportions of ancient fallow deer indicate the gradual changes of the ecological conditions during the Farneta Faunal Unit and the Pirro Faunal Unit (terminal part of the late Villafranchian) toward the more open and dry type of savannah, the savannah parkland and tree-shrub savannah (CROITOR, 2001).

Metacervoceros rhenanus is an early Villafranchian holdover. The morphology of antlers and skull suggest that this fossil deer was similar or even very close to the actual deer of the genus *Axis*. The distribution of *M. rhenanus* at the middle-late Villafranchian boundary was more extensive and included Italy (Olivola Faunal Unit), France (Sent Vallier) and Romania (Milcovu din Vale). During the late Villafranchian, the area of distribution of *M. rhenanus* became restricted to the Central and Northern France and Holland (CROITOR & BONIFAY, 2001). Perhaps, the climate aridization in South Europe during late Villafranchian was a limiting ecologic factor for *M. rhenanus* distribution. The simultaneous presence of *D. vallonnetensis* and *M. rhenanus* in the archaeological site of Vallonnet may be explained by the preferences of ancient humans to settle in ecotones were the species from different ecosystems can meet. The fallow deer represented by very scant remains in Ceyssaguet, apparently, is a seasonal immigrant from the Mediterranean area. KAISER & CROITOR (in press) supposed that the valley of the ancient Rhone River is a likely way for those migrations, as only few dozens of km separate the modern Rhone valley and the site of Ceyssaguet.

CONCLUSIONS

The early Pleistocene small-sized deer of Europe belong to three different genera *Cervus*, *Dama* and *Metacervoceros*. Villafranchian *Cervus* are represented by two species: the more primitive *C. abesalomi* from Georgia and *C. nestii* from Italy. Such characters of cranial morphology as the long orbito-frontal portion of face and the short predental part approach *C. nestii* to the actual primitive form of red deer *C. elaphus bactrianus*. The antlers of *C. nestii* and *C. abesalomi* with the single brow tine, the trez tine and the distal transversally oriented fork are similar to *C. elaphus barbarus*. The morpho-functional and ecological adaptations suggest *C. nestii* as a forest inhabitant that could live in the mountain landscape.

D. eurygonos is characterised by the short incranial pedicles, the flexed and rounded braincase, large orbits, very large ethmoidal openings and short face as actual *D. dama*. The antlers are simple with a basal tine with very open angle of ramification, a weak middle tine that has an evolutionary trend to disappear and a distal ramification situated in a parasagittal plane. The latest Villaf r a n c h i a n species *D. vallonnetensis* is characterised by three-pointed for the second tine antlers due to the loss of the middle tine. The species preferred more open and dry habitats.

M. rhenanus represents the most primitive lineage of the early Pleistocene small-sized deer close to modern *Axis*. It is characterised by the very long and unflexed braincase, long and sloped toward the posterior pedicles, short orbito-frontal part of the skull, primitive dentition and tree-pointed antlers. The species preferred more humid envitonment. The diagnostic characters of the late Villafranchian small-sized deer are summarized in the Table 11.

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REFERENCES

- ABBAZZI, L. (1995). Occurrence of palmed *Cervus elaphus* from Italian late Pleistocene localities. *Atti della Accademia Nazionale dei lincei, Science fisiche e naturali*, ser. 9, 6 (3), 189-206, Rome.
- ABBAZZI, L. (2001). A revision of medium and small sized deer from the middle and Late Pleistocene of Calabria and Sicily. *Bolletino della Societa Palaeontologica Italiana*, 40 (2), 115-126, Modena.
- ALEXEEVA, L.I. (1977). Theriofauna of Eastern Europe Early Anthropogene (in Russian). *Transactions of the Institute of Geology*, 300, 3-108, Moscow.
- AZZAROLI, A. (1947). I cervi fossili della Toscana. Palaeonto graphia Italica, 43, 46-81, Pisa.
- AZZAROLI, A. (1953). The deer of the Weybourn Crag and Forest Bed of Norfolk. *Bull. Brit. Mus. (Nat. Hist.), Geology*, 2 (1), 1-96, London.
- AZZAROLI, A. (1961). Il nanismo nei cervi insulari. Palaeonto graphia Italica, 26, 1-31, Pisa.
- AZZAROLI, A. (1992). The cervid genus *Pseudodama n.g.* in the Villafranchian of Tuscany. *Palaeontographia Italica*, 79, 1-41, Pisa.
- BOEUF, O., GERAADS, D. & C. GUTH (1992). Cervides Villafranchiens de Blassac-la-Girondie (Haute-Loire, France). Annales de Paleontologie, 78 (3), 159-187.
- BOUT, P. & A. AZZAROLI (1952). Stratigraphie et Faune du creux de Peirolles pres Perrier (Puy-de-Dôme. *Annales de Paléontologie*, 38, 3-22, Paris.
- Caro, T.M., GRAHAM, C. M., STONER C. J. & M. M. FLORES (2003). Correlates of horn and antler shape in bovids and cervids. *Behaviour*, *Ecology*, *Sociobiology*, 55, 32-41.
- CROITOR, R. (2001). Functional morphology of small-sized deer from the early and middle Pleistocene of Italy, implication to the paleolandscape reconstruction. La Terra degli Elefanti, Proceedings of the First International Congress, 97-102, Rome.
- CROITOR, R. & M.-F. BONIFAY (2001). Étude préliminaire des cerfs du gisement Pleistocène inférieur de Ceyssaguet (Haut-Loire). *Paleo*, 13, 129-144.
- CROITOR, R. & Th. KAISER (2002). Functional morphology and diet preferences of fossil deer and paleolandscape reconstruction of early Pleistocene of Ceyssaguet. *Verhandlungen der Gesell schaft für Okologie*, Band 32, 465. Cottbus.
- CROITOR R. & K. STEFANIAK (in press). Pliocene deer of Eastern Europe. *Palaeontographica*.
- CUENCA-BESCOS, G. & N. GARSIA (2004). Mammalian distributions in the Trinchera Dolina sequence (Lower to middle Pleistocene, Atapuerca, Spain). Late Neogene and Quartenary biodiversity and evolution, Regional developments and interregional correlations. 18th International Senckenberg Conference, 91-92.
- CZYZEWSKA, T. (1968). Deer from Weze and their relationship with the Pliocene and recent Eurasiatic Cervidae. Acta Palaeontologica Polonica, 13 (4), 537-590, Warszawa.
- DE GIULI, C. (1986). Late Villafranchian Faunas in Italy, the Selvella Local Fauna in the southern Chiana Valley – Umbria.

Palaeontographia Italica, 74, 11-50, Pisa.

- DE GIULI, C., MASINI, F. & D. TORRE (1986). The latest Villafranchian faunas in Italy, the Pirro Nord Fauna (Apricena, Gargano). *Palaeontographia Italica*, 74, 56-62, Pisa.
- DIETRICH, W.O. (1938). Zur Kenntnis der oberpliocaenen echten Hirsche. Zeitschrift de Deutschen Geologischen Gezellschaft, 90 (5), 261-267, Berlin.
- DI STEFANO, G. (1995). The Mesopotamian fallow deer (*Dama*, Artiodactyla) in the Middle East Pleistocene. *N. Jb. Geol. Palaeont. Abh.*, 199, 295-322, Stuttgart.
- DI STEFANO, G. & C. PETRONIO (1992). Nuove osservazioni su Cervus elaphus acoronatus Beninde del Pleistocene europeo. Bolletino della Societa Paleontologica Italiana, 31 (3), 295-315, Modena.
- DI STEFANO, G. & C. PETRONIO (1997). Origin and evolution of the European fallow deer (*Dam a*, Pleistocene). N. Jb. Geol. Palaeont. Abh., 203, 57-75, Stuttgart.
- DI STEFANO, G. & C. PETRONIO (1998). Origin and relationships among *Dama*-like cervids in Europe. *N. Jb. Geol. Palaeont. Abh.*, 207, 37-55, Stuttgart.
- FLEROW, K.K. (1952). Musk deer and deer (in Russian). Fauna of the USSR. Mammalia, 1(2), 3-255, Moscow-Leningrad.
- FLEROW, K.K. (1962). Family Cervidae GRAY 1821 (in Russian). *Osnovy paleontologii*, 13, 368-378. Moscow.
- GAMBARIAN, P.P. (1972). The Running of Mammals. Adaptation features of locomotion organs (in Russian), 3-331, Leningrad.
- GEIST, V. (1987). On speciation in Ice Age mammals, with special reference to cervids and caprids. *Canadian Journal on Zoology*, 65 (5), 1067-1084, Edmonton.
- GEIST, V. (1998). *Deer of the World, Their Evolution, Behavior and Ecology*. 1-421, Stackpole Books.
- GIROTTI, O., CAPASSO BARBATO, L., ESU, D., GLIOZZI, E., KOTSAKIS, T., MARTINETTO, E., PETRONIO, C., SARDELLA, R. & E. SQUAZZINI (2003). The section of Torre Picchio (terni, Umbria, Central Italy), a Villafranchian site rich in Vertebrates, molluscs, ostracods and plants. *Rivista Italiana di Paleontologia e Stratigrafia*, 109 (1), 77-98.
- GUADELLI, J.-L. (1987). Contribution a l'étude des zoocénoses préhistoriques en Aquitaine (Wurm ancien et interstade wurmien). *Thèse de docteur, l'Université de Bordeaux I*, 1-300.
- HEINZ, E. (1970). Les Cervides Villafranchiens de Franse et d'Espagne. *Memoires du Museum national d'histoire naturelle*. Ser.C, Sc. De la Terre, 22 (1-2), 1-302, Paris.
- HEPTNER, V.G. & V.I. TZALKIN (1947). Deer of the USSR (in Russian). *Transactions on Study of Fauna and Flora of the USSR*, 10 (25), 1-176, Moscow.
- HUSAK, F. (1986). Danek. In, Danek / Sika / Jelenec, 9-148, Praha.
- JANIS, C.M. (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. *In:* DAMUTH J. & B.J. MAC FADDEN (*Eds*), *Body size in mammalian paleobiology. Estimation and biological implications*. Cambridge University Press, Cambridge; 255-300.
- JANIS, C.M. & A. LISTER (1985). The morphology of the lower fourth premolar as a taxonomic character in the ruminania (Mammalia, Artiodactyla), and the systematic position of Triceromeryx. *Journal of Paleontology*, 59 (2), 405-410.
- KÖHLER, M. (1993). Skeleton and Habitat of fossil and recent Ruminants. *Munchner geowiss*. Abh. (A), 25, 1-88, Munich.
- KAHLKE, H.-D. (1997). Die Cerviden-reste aus dem Unterpleistozän von Untermassfeld. Das Pleistozän von Untermassfeld bei Meningen (Thüringen), Teil 1. Monographien des Römisch-Germanischen Zentralmuseums Mainz, 40 (1), 181-275.
- KAHLKE, H.-D. (2001). Neufunde fon Cerviden-resten aus dem Unterpleistozän von Untermassfeld. Das Pleistozän von Untermassfeld bei Meningen (Thüringen), Teil 2. Monographien des Römisch-Germanischen Zentralmuseums Mainz, 40 (2),

461-482.

- KAISER, Th. & R. CROITOR (in press). Grazing Deer from the early-Pleistocene of Ceyssaguet (Haute-Loire, France). *Geobios*.
- KOROTKEVICH, E.L. (1970). The late Neogene deer from North Black sea area. 1-175, Kiev.
- LISTER, A.M. (1990). Critical reappraisal of the middle Pleistocene deer "*Cervus*" *elaphoides* KAHLKE. *Quaternaire*, 3-4 , 175-192.
- LUDT, Ch., SCHROEDER, W., ROTTMANN, O. & R. KUEHN (2004). Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Molecular Phylogenetics and Evolution*, 31, 1064-1083.
- LUMLEY DE, H., KAHLKE, H.-D., MOIGNE, A.-M. & P.-E. MOULLÉ (1988). Les faunes de grands mammiferes de la grotte du Vallonnet Roquebrune-Cap-Martin, Alpes-Maritimes. L'Anthropologie, 92 (2), 465-496, Paris.
- MADE, J. VAN DER, (1999). On *Euraxis*, on the rules of the ICZN, on methodology. *N. Jb. Geol. Palaeont. Mh.*, (11), 676–678, Stuttgart.
- MARKOV, G.G. & A.A. DANILKIN (1999). Geographic craniometric variability and intraspecific taxonomy of the red deer (*Cervus elaphus* L.) in Palearctic. *Advances in Deer Biology*, 119-120, Kaposvar.
- PETRONIO, C. (1979). Dama nestii eurygonos Azz. di Capena (Roma). Geologica Romana, 18, 105-125, Rome.
- PIDOPLICZKO, N.G. & K.K. FLEROW (1952). The new form of deer from Pliocene of Southern Ukraine. *Reports of the Academy of Sciences of USSR*, 84 (6), 1239-1242.
- PFEIFFER, Th. (1997). Dama (Pseudodama) reichenaiui (KAHLKE, 1996) (Artyodactyla, Cervidae, Cervini) aus den Mosbach-Sanden (Wiesbaden-Biebrich). Mainzer Naturwiss. Archiv, 35, 31-59.
- PFEIFFER, Th. (1998). Die fossilen Damhirsche von Neumark Nord (Sachsen-Anhalt) – D. dama geiselana n. ssp. Eiszeitalter U. Gegenwart, 48, 72-86, Hannover.
- RADULESCO, C. & Z. KISGYORGY (1970). Contribution a la connaissance de la faune de mamiferes Villafranchiens de Capeni-Virghis (Depression de Brasov). *Aluta*, 1970, 11-22.
- RANDI, E., MUCCI, N., PIERPAOLI, M. & E. DOUZERY (1998). New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome *b* gene. *Proceedings of Royal Society of London*, 265, 793-801.
- REUTERSHAN, T., TIEDEMANN, R., HARTL, G.B. & M. APOLLONIO (1999). Origin of sardinian red deer (*Cervus elaphus corsicanus*) as revealed by sequence analysis of mtDNA-control region. *Advances in Deer Biology*, 200, Kaposvar.
- SOKOLOV, I.I. (1959). Hoofed animals (Perissodactyla & Artiodactyla) (in Russian). *Fauna of the USSR. Mammalia*, 1 (3), 3-639, Moscow.
- SOKOLOV, I.I., KLEBANOVA, E.A. & A.S. SOKOLOV (1964). Morpho-functional peculiarities of locomotion apparatus of Saiga and Jeiran (in Russian). Morphology of vertebrate animals, Transactions of the Zoological Institute, 33, 319-347, Moscow-Leningrad.
- SPAAN, A. (1992). A revision of the deer from Tegelen (Province of Limburg, The Netherlands). Scripta Geologica, 98, 1-42.
- SPENCER, L. (1995). Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy*, 76 (2), 448-471.
- SUTULA, V.A. (1990). Adaptation significance of proportions of the ungulates (in Russian). Morphology of mammals and problems of locomotion. Transactions of the Zoological Institute, 215, 137-151, Leningrad.
- VISLOBOKOVA, I.A. (1990). Fossil deer of Eurasia (in Russian). Transactions of the Paleontological Institute, 240, 1-206,

Moscow.

VOS J. DE, MOL, D. & J. W.F. REUMER (1995). Early pleistocene Cervidae (Mammalia, Artyodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros* FALCONER, 1868. Deinsea, 2, 95-121.

WOLF, R. (1986). Jelen sika. In: Danek / Sika / Jelenec, 149-228, Praha.