

Functional morphology of small-sized deer from the Early and Middle Pleistocene of Italy: implication for paleolandscape reconstruction

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SUMMARY: The functional morphology of antlers, masticatory apparatus and appendicular skeleton of the early and middle Pleistocene small-sized deer *Pseudodama nestii* and ancient species of the genus *Dama* is regarded in the present paper. The revealed morpho-functional adaptations suggest *P. nestii* as an inhabitant of mountainous forests. *Dama eurygonos*, *D. eurygonos farnetensis* and *D. vallonnetensis* that form a phyletical lineage, inhabited open savanna-like landscapes and display gradual evolutionary changes in the direction of ritualised antlers and cursorial locomotion. The functional morphology and ecology of the studied deer suggest the changes of the ecological conditions during the late Villafranchian from mixed forest-savanna landscape to the more open and dry type of savanna, the savanna parkland and tree-shrub savanna.

1. INTRODUCTION

Cervids are an important back-ground faunal group represented by numerous species and well-preserved fossil remains and may be a valuable tool in the Villafranchian paleolandscape reconstruction. Several phylogenetical lineages of small-sized deer are recorded in the Early Pleistocene deposits of Italy. The first lineage contains a single species *Pseudodama nestii* (Azzaroli 1947) that is evolutionary close to recent representatives of the genera *Axis* and *Cervus*. *P. lyra* Azzaroli 1992 shows a rather early ontogenetical stage of antler development and should be considered as a junior synonym of *P. nestii* (Croitor in press). The second lineage includes ancient fallow deer *Dama eurygonos* Azzaroli 1947, a larger advanced subspecies *D. eurygonos farnetensis* Azzaroli 1992 and *D. vallonnetensis* (= *Cervus s.l. nestii vallonnetensis* de Lumley *et al.* 1988). The Villafranchian fallow deer are characterised by typical for *Dama* cranial morphology, however their antlers lack the distal palmation. Both *P. nestii* and *D. eurygonos* are discovered in the composition of the fauna

from Figline (Tasso F.U.) (Croitor in press), dated by the beginning of early Pleistocene of Italy (Azzaroli 1992). *D. e. farnetensis* is the best represented species in the Farneta F.U. that is the next stage of the Villafranchian fauna development (De Giuli 1986). *D. vallonnetensis* is recorded in the latest Villafranchian – Postvillafranchian faunas of Italy and South France. In Italy, the remains of this deer are recorded in the composition of Pirro F.U. from Capena (reported as *Dama nestii eurygonos* by Petronio 1979) and Pirro Nord (= "*Dama*" cf. *nestii*: De Giuli *et al.* 1987, = *Pseudodama farnetensis*: Colucci 1993). Pfeifer (1997) and Di Stefano & Petronio (1998) made recent attempts of systematical revision of the Villafranchian small-sized deer based mainly on the morphology and proportions of appendicular skeleton. However, the systematical value of postcranial limbs is a matter of doubts in this case. The postcranial morphology suggests the ecological adaptations and locomotion strategy of the species and depends of the landscape character and the body weight (Sokolov *et al.* 1964; Gambaryan 1970; Sutula 1990) and, as it was already mentioned, has no

any certain systematical significance. The studied fossil material includes complete skeletons or articulated parts of skeletons discovered in the Villafranchian and Postvillafranchian deposits of Italy. The postcranial remains of *D. eurygonos farnetensis* from Selvella are associated with the antlers and dentition (De Giuli 1986). The Selvella material allowed to separate the postcranial bones of *D. eurygonos* and *P. nestii* from Upper Valdarno and to associate them with antlers and skulls.

2. MORPHOLOGICAL DESCRIPTION

2.1 *Pseudodama nestii*

The antlers are rather thin and four-pointed, with basal and trez (middle) tines. The distal bifurcation formed by two tines of equal size, is oriented transversally to the sagittal plane (Azzaroli 1947). Pedicels are long and sloped backward from the face. The facial part of skull is long, however the praedental portion is relatively short. The cranial proportions (the long orbito-frontal part, the long facial portion) and some details of antler morphology (such as the frontally oriented distal fork) suggest this deer may be related to primitive modern and fossil deer of the *elaphus* group from the Western Mediterranean region, such as *Cervus arretinus*, *C. elaphus corsicanus*, *C. e. barbarus* and *C. e. hispanicus*. The lower praemolar series is comparatively long, the morphology of P_4 is primitive. The forelimb is characterised by a relatively short metacarpus, which is shorter than radius (the metacarpus/radius length ratio amounts to 92.5 %). The proximal end of the radius is comparatively wide. The lateral portion of articulation surface 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. The incision for articulation with *processus coronoideus* of ulna is comparatively deep. The distal portions of metapodial bones are sharply broadened, so the distal epiphyses has a triangular shape. The proximal phalanxes are very long and robust,

while the medial phalanxes are relatively small.

2.2 *Dama eurygonos*

The four-pointed antlers generally are more robust and stronger bent sideways if compared to *P. nestii*. The trez tine is comparatively small and occurs only in fully grown mature individuals. The two terminal tines are very long and form the bifurcation oriented in a parasagittal plane. The general morphology of skull and dentition is similar to the modern fallow deer. The braincase is short and domed, the orbito-frontal part is short, the pedicels are short and incranial. P_4 is molarised, the lower praedental series is short if compared with that of *P. nestii*. The nasal bones does not reach behind the line connecting the frontal edges of orbits, unlike modern *D. dama*. The proximal epiphysis of radius is narrowed if compared to one of *P. nestii*. The area of medial portion of the proximal articulation surface of radius is particularly diminished if compared to *P. nestii*, while the *epicondylus lateralis* is stronger. The incision for the articulation with *processus coronoideus* of ulna is shallow. The studied articulated forelimb is characterised by a comparatively long metacarpus, which is almost of the same length as the radius (the metacarpus/radius length index amounts to 98.6 %). The distal epiphysis of metacarpus is not broadened as sharp as in *P. nestii*. The metatarsal bone is long, its proximal epiphysis is narrow and deep. Proximal phalanxes are weak and very short if compared to *P. nestii*.

2.3 *Dama eurygonos farnetensis*

The deer under discussion is larger if compared to *D. e. eurygonos* from Upper Valdarno, its antlers are characterised by a very long curved first tine inserted at a certain distance from the burr. The antler beams are robust and strongly divergent, becoming horizontal in a section between the brow and the trez tine. Metapodials are relatively longer if compared to *D. eurygonos*. The ratio between length of metacarpus and radius (the mean value) amounts to 101.0 %.

2.4 *Dama vallonnetensis*

The antlers are very robust, however, they lack the trez (middle) tine, possessing only a very long and strong basal tine situated right above the burr and a distal bifurcation formed by two long tines oriented in the parasagittal plane. The skull morphology is typical for the genus *Dama*, however, unlike *D. dama*, the nasal bones does not reach behind the line connecting the anterior edges of orbits, the connection between nasal and praemaxillary bones is long. The praemaxillary bones are broadened and robust if compared to the modern fallow deer, the praedental portion is comparatively long. The relative metapodial length of *D. vallonnetensis* is similar to that of *D. eurygonos farnetensis*.

2.5 *Dama clactoniana*

D. clactoniana is a middle Pleistocene representative of the genus, characterised by the largest size and palmed antlers. Some interesting morphological peculiarities of this deer deserve to be mentioned here. The cranial material from Swanscombe (England) and Riano (Italy) display a morphology of facial bones, similar to the Villafranchian fallow deer such as the position of posterior edge of nasal bones and the long connection between praemaxillary and nasal bones. The facial morphology allows us to assume that *D. clactoniana* belongs to the same phyletical stock as the Villafranchian fallow deer. The complete articulated skeleton from Riano (Leonardi & Petronio 1976) is characterised by a very long distal part of limbs. The radius/metacarpus length ratio of the fallow deer from Riano amounts to 103.3 %.

3. MORPHO-FUNCTIONAL ANALYSIS

3.1 Comparison of *P. nestii* and *D. eurygonos*

The molarisation of praemolars and shortened praemolar series are two ways of adaptation to the tougher grass forage in ruminants (Vislobokova 1990; Spencer 1995). Both ways

of adaptation increase the length of the grinding tooth surface. It may be achieved by the relative increasing of the molar grinding surface length that is followed by the praemolar length reducing, or the advanced molarisation of praemolars, which in this case work physiologically as molars. One can follow the both extreme variants of these morphological adaptations among Cervidae, for example, the very long praemolar series with highly molarised P₄ and P₃ in *Alces* and the very short and primitive praemolars in some Villafranchian *Eucladoceros*. The lower dentition of *D. eurygonos* shows a combination of molarised P₄ and the shortened praemolar row that may suggest the adaptation to a more or less coarse food. However, the *corpus mandibulae* remains shallow and slender, the fact suggesting that the species under consideration could not be a real grazer and may be classified as a mixed feeder.

The lower dentition of *P. nestii* maintains the primitive proportions with longer praemolar series and the simple morphology of praemolars. According to Spencer (1995), a long praemolar series is critical in processing dicotyledon material, because the praemolars, with their well-developed shearing crest, are used for slicing and puncture crushing of the soft juicy herbage. Among morphological characters of the so-called dicot feeders, Spencer (1995) mentioned the short preedental portion of skull and narrow premaxillary bones. Unfortunately, the premaxillary bones in the single available complete skull of *P. nestii* from Figline are deformed, however, the remarkably short preedental part of skull and relatively long lower praemolar series suggest this deer as a browser.

The ratio between limb segments in hoofed animals and their detailed postcranial morphology were used by many authors in study of the locomotion type and the landscape character (Egorov 1955; Sokolov *et al.* 1964; Gambaryan 1972; Sutula 1990; Köhler 1993). *D. eurygonos* has comparatively long metapodials and small and short phalanxes. The metapodial bones do not change their thickness distally much, unlike *P. nestii*. The articulation surfaces of distal

metapodial epiphyses are high and narrow. The distal intertrochlear incision of metapodials is narrow. The enlisted characters are interpreted by Köhler (1993) and Sokolov *et al.* (1964) as the adaptation to open, flat and dry habitats.

P. nestii is characterised by short metapodials, conspicuously large proximal phalanxes and wide long bone epiphyses. The possibility of correlation between the short metapodials and the short prepedal part of skull should be ruled out in this case, as the short prepedal portion in *P. nestii* is combined with relatively long face, and the reduced metapodial length is combined with long phalanxes. The distal epiphysis of metapodials are broadened sharply, the distal articulation surfaces are low if compared to *D. eurygonos*. The long radius and short metapodial bones are considered as adaptations to the saltatorial locomotion in wooded habitats (Gambaryan 1972; Sutula 1990). The short metapodial bones, the strongly broadened epiphyses of long bones are suggested as adaptations to wooded and mountainous landscapes (Egorov 1955; Köhler 1993).

The deep incision for *processus coronoideus* on the proximal epiphyses of radius observed in *P. nestii* apparently makes stronger the connection between radius and ulna and was suggested as an adaptation to the increased dynamic load upon the elbow joint (Croitor 1997). Gambaryan (1972) and Egorov (1955) reported the increased functional load upon elbow joint in ruminants adapted to mountainous habitats. One can suppose that the increased power load in the forelimbs in combination with short metapodials in *P. nestii* may suggest the adaptations to more or less mountainous landscape.

The large and very robust proximal phalanx and the strong middle phalanx with prominent plateau postarticulaire (Köhler 1993) suggest *P. nestii* as a typical woodland dweller. The phalanxes of *D. eurygonos* are much slender. The proximal phalanx is characterised by the deep incision of the proximal epiphysis for the articulation with metapodial verticulus. The middle phalanx has the comparatively weak plateau postarticulaire. Köhler (1993) regarded such a morphological pattern of phalanxes as the adaptation to open and dry habitats.

2.2 Evolutionary trends and ecology of the early Pleistocene fallow deer

The evolutionary change in antler morphology of Villafranchian fallow deer concerns the reduction of trez tine and obviously should be interpreted in the context of the relationship between the social behavior and the antler shape. This tine is quite weak in *D. eurygonos* if compared to *P. nestii* and occurs only in fully-grown antlers of adult individuals. *D. vallonnetensis*, the descent of *D. eurygonos*, completely lost this tine and is characterized by the three-pointed antlers for a second time. One can assume that 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. We can assume that the loss of the trez tine followed the change in rutting behavior of ancient fallow deer and, as a consequence, the change of the antler function. Perhaps, the simplified, but comparatively large antlers of *D. vallonnetensis* served mainly the function of social display and the antler function as an effective weapon was insignificant. The comparatively large size of antlers and their ritualised function may be interpreted as an adaptation of Villafranchian fallow deer to a more or less open landscape (Geist 1971, Köhler 1993). The long praedental part and broad praemaxillar bones of the fallow deer from Pirro Nord were regarded by Colucci (1993) as another adaptation to the coarse grass forage in the dry open landscape conditions.

The study of limb proportions revealed a gradual lengthening of the metapodial bones in the phyletical lineage *D.e. eurygonos* – *D.e. farnetensis* – *D. vallonnetensis* – *D. clactoniana*. The metacarpus has almost the same length as the radius in *D. eurygonos*, while in more advanced *D. eurygonos farnetensis* the metacarpal bone is longer than the radius. The relatively longest metapodial bones are recorded in the middle Pleistocene *D. clactoniana*. These changes in the limb proportion of fossil fallow deer are not correlated with the increased body size. Gambaryan (1972) reported a correlation between the larger body size and the short distal portions of appendicular

skeleton. The study of individual variation of the modern *D. dama* revealed the similar correlation, as the smaller individuals (mainly females) has the longer metapodials. The limb proportions of the Villafranchian *Dama*, and particularly of the middle Pleistocene *D. clactoniana*, approach to those of the modern antelope *Gazella subgutturosa*, an open landscape inhabitant, which developed adaptations to cursorial locomotion in the conditions of open shrubland (Sokolov *et al.* 1964, Sutula 1990).

3. PALEOLANDSCAPE RECONSTRUCTION

The functional morphology study allows us to consider *P. nestii* as a forest dweller adapted to locomotion in the mountainous landscape. *D. eurygonos* displays adaptations typical of a cursorial runner and inhabited open landscape with woody vegetation. Both the deer species are important back-ground elements of the Tasso FU and suggest the mixed character of landscape with mountainous forests and more open and dry landscape of the savanna woodland type (according to the terminology of Cole 1963) in the lowlands. The evolutionary trends in antler morphology and limb proportions of ancient fallow deer indicate the gradual changes of the ecological conditions during the Farneta FU and the Pirro FU (terminal part of the late Villafranchian) toward the more open and dry type of savanna, the savanna parkland and tree-shrub savanna.

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