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THE HOLOTYPE OF *CERVALCES GALLICUS* (AZZAROLI, 1952) FROM SÉNÈZE (HAUTE-LOIRE, FRANCE) WITH NOMENCLATURAL IMPLICATIONS AND TAXONOMICAL-PHYLOGENETIC ACCOUNTS.

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Riassunto. In questo lavoro vengono riesaminati i resti di *Cervalces (Libralces) gallicus* (Azzaroli, 1952) provenienti dal giacimento del Villafranchiano medio-superiore di Sénèze (Alta Loira, Francia) e custoditi presso il Museo Paleontologico dell'Università Claude Bernard - Lyon 1. Si tratta di uno scheletro montato, completo di cranio con palchi e tutti gli elementi postcraniali, descritto come olotipo da Azzaroli (1952), e dello scheletro degli arti di un secondo individuo, indicato dallo stesso autore come cotipo.

Si attribuisce qui all'olotipo lo scheletro degli arti del secondo individuo, mentre gli arti montati, di minori dimensioni, per il loro pessimo stato di conservazione non si prestano ad una determinazione che vada oltre al rango tassonomico di famiglia. Si discutono quindi i caratteri determinanti il genere *Cervalces* e si concorda con Azzaroli nell'attribuirgli anche la specie *C. (L.) latifrons*, del Pleistocene medio-superiore. Tutte le specie del genere *Cervalces* presentano caratteri della morfologia cranica e facciale che si discostano notevolmente da quelli dell'attuale *Alces*. L'occipitale stretto e alto ed i nasali brevi non a contatto con i lunghi premascellari, sono quindi considerati caratteri apomorfi della sola specie *Alces alces*.

Abstract. The remains of *Cervalces (Libralces) gallicus* (Azzaroli, 1952) from the Middle-Upper Villafranchian of Sénèze (Haute-Loire, France), kept in the Paleontological Museum of the University Claude Bernard - Lyon 1, are here studied again. The remains consist of an assembled skeleton, with skull, antlers and all postcranial elements, described by Azzaroli (1952) as holotype, and in the limb bones of a second specimen, designated as cotype by the same author. The cotype's limb bones are here attributed to the holotype, while the smaller assembled limb bones cannot be determined over the family taxonomic level, due to the bad state of preservation.

The characters determining the genus *Cervalces* are described here and, in accordance with Azzaroli, the species *C. (L.) latifrons* from the Middle-Upper Pleistocene is attributed to it. All the species of the genus *Cervalces* show characters of cranial and facial morphology, which differ from that of present-day *Alces*. The narrow, deep occipital and the short nasals, not articulated with the long premaxillaris, are in this view considered apomorphic characters of *Alces alces*.

Introduction

The Geological Department of the University Claude Bernard - Lyon 1, houses the holotype of *Cervalces (Libralces) gallicus* (Azzaroli, 1952) found in the early twenties in Sénèze (Domeyrat, Haute-Loire, France) and reported as elk since 1931 by Roman and Dareste de la Chavanne. The holotype consists of an adult male, with part of the antlers and the whole skeleton, mounted but showing heavy damage in all its elements.

The age of Sénèze deposit is still being debated. Azzaroli et al. (1988) consider two distinct mammal faunas, the former from the end of the Middle Villafranchian (with *Eucladoceros senezensis*), the latter from the Upper Villafranchian (with *C. gallicus*). Most articulated skeletons come from the older unit, a "maar" deposit. Lister (1993a) suggests that the skeleton of *C. gallicus*, for its completeness, should belong to this lacustrine succession, dated, by palaeomagnetic studies (Thouveny & Bonifay, 1984), to 2.0-1.6 myr BP. Lister's suggestion is accepted here because it better agrees with the age of the other remains of *C. gallicus* from Europe.

Azzaroli, in a revision of the Cervids from the English Forest Bed (Azzaroli, 1953), was unable to correlate skulls, jaws and limb bones of several species of elks, very different from present-day elk (Azzaroli, 1952, pp. 133). He therefore described a new genus and a new species, *Libralces gallicus*, based on the specimen from Sénèze, clearly not well preserved, but substantially complete. Later Azzaroli (1982) downgraded *Libralces* to subgenus of *Cervalces*, genotype the North American *Cervalces (Cervalces) scotti* (Lydekker, 1898).

Unfortunately the whole skeleton of the holotype from Sénèze is badly deteriorated and has undergone heavy restoration that has altered its physiognomy. In particular, numerous missing parts have been reconstructed and the whole covered with a dark brown paint that makes it impossible to distinguish original portions from reconstructed ones.

As the holotype is fragmentary, Azzaroli (1952) referred to the samples from the English Forest Bed for

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the description of the neurocranium and jaw. These remains, kept in the Natural History Museum of London, are a skull (M6101) and two jaws (M6206 and M6229) from the Weybourn Crag of East Runton. The skull from Sénèze retains, however, the facial portion, not present in all the English remains, that shows some peculiar morphologies which justify the new genus and the choice of the holotype.

For the description of postcranial elements, Azzaroli (1952) referred to the limb bones of a second specimen, kept in the Lyon University Museum coming, probably, from the same area (no documentation of its finding exists).

The aim of this work is to describe the skull of the holotype in greater detail, with reference to English specimens purely for comparison or additional information. The limb bones are also analysed here, for comparison with present-day elk.

Preliminary considerations and nomenclatural implications

In studying the assembled skeleton, it was impossible to distinguish the original portions from those reconstructed in plaster. This problem, already remarkable for the cranial elements, was even greater for limb bones. Left tibia, left humerus, carpal and tarsal bones are totally reconstructed; right tibia, right humerus, metapodials, phalanges, radii and ulnas possess some original bony parts which are unrecognisable from the reconstructed ones. Pfeiffer (pers. comm., 2001) suggests that some of these bones may belong to *Eucladoceros.*

Limb bones, described by Azzaroli (1952) as cotype, are in far better condition. Some long bones have been repaired, but simply by joining fractured diaphyses. Bones are very light with traces of red clay soil; some elements of carpus and tarsus are blackened by combustion. The amazing completeness of the cotype limbs would suggest that it was found in anatomic connection. As a matter of fact there are: all the phalanges, all the carpal elements except the right pisiform, all the tarsal elements except the left malleolus and small cuneiforms, and all the long bones except femurs. The striking complementarity of the bone elements of the cotype with the only ones of the assembled skeleton, which are not totally reconstructed (scapulas, pelvis and femurs), together with the same kind of fossilization, would suggest that they belong to the same specimen.

Azzaroli (1952, pp. 133) writes: "According to Prof. Viret (the current director of the Geological Department of Lyon) the skeleton was disassembled and protected during the war; the current assembling, very imperfect, is provisional...". So, it is possible that, when the skeleton was "temporarily" assembled after the war, the original limb bones were not used. These bones, being of smaller size, could belong to a female of the same species; they lack, however, morphological elements that would support this hypothesis.

The limbs now assembled are excluded here from the holotype, as per rule 73.1.5 of the 4th edition of the "International Code of Zoological Nomenclature" (rule 73.1.5 refers exactly to holotypes consisting of a set of disarticulated body parts found not deriving from an individual animal).

The limb bones described by Azzaroli (1952) as cotype are here attributed to the holotype. This case has never been submitted to the International Commission on Zoological Nomenclature until now (Minelli, pers. comm., 2000) and there are no rules concerning exactly such a case. Rule 75.8, referring to the status of rediscovered former name-bearing types that were presumed lost, may be applied to this case by analogy.

Follows a description, as careful as possible, of the holotype as defined above. The nomenclature of Barone (1980) is used here.

Description

Antlers

A long slender beam departs from the broad frontals, with no sign of bifurcation or tines, and flattens out at its extremities into wide palmations. Both antlers were cut at the burr and assembled on a metallic support. The lack of complementarity between the vertical surfaces of the two stumps, due to the loss of a portion of beam during cutting, makes it difficult to hypothesise the exact original orientation of the antlers.

In the current assemblage the two beams are gently twisted, the left clockwise and the right counterclockwise, and widen in a vertical palmation with posterior concavity. Both antlers retain the lower tine downward and posteriorly directed; the right antler retains the base of a second tine. Then the palmations extend outwards and upwards but are broken off without other tines. It is impossible to hypothesise the original total span of the antlers, however each one of them shows an overall length of over one meter. Therefore, including the width of the skull, the total span may be calculated about 2 meters and 235 mm.

Skull

The skull is formed by the neurocranial and the facial portion united by a plaster bridge, modelled in a rather arbitrary way. It is impossible to reconstruct the value of the cranio-facial angle, but it should have been closer than in the current restoration, with the occipital more vertically set, as shown in Fig. 1 (modified from Azzaroli's original). It is difficult to hypothesise the total length of the skull, which, in present restoration, is

500 mm from the premaxillary tip to the occipital posterior edge.

The lateral insertion of antlers is one of the most typical characters of Alcini. In the studied specimen, the pedicles point horizontally out from the wide frontals. Moreover, the pedicles show an elliptical section, dorsoventrally compressed, and the burr is set obliquely to the axis of the beam. The frontals, quite integral, are more convex than in present-day elk, but the suture lines are totally hidden by paint.

The occipital, in nuchal view, is broad and shallow, more similar to that of other Cervids than to present-day elk, which is narrow and deep (Azzaroli 1952, 1979, 1982).

A portion of the right jugular process and auditory duct are preserved. The basioccipital, wide and short, ends forward in the basal tubercle and lacks the bordering basisphenoid body. Condyles and foramen magnum have very poorly preserved surfaces, but the sagittally elongated outline of the condyles is still evident.

The facial skull is badly deformed and has undergone heavy restoration but shows peculiar characters that justify the attribution to a genus different from *Alces*. As a matter of fact, the skull from Sénèze shows long nasals (75 mm from nasion to rhinion) articulated with the short praemaxillae (the left, 152 mm and the right, 170 mm for face deformation). This facial structure is intermediate, in bone proportions, between the extremely specialized one of *A. alces* and the more general one of *Cervus* and *Megaloceros.* Azzaroli (1979) hypothesised that the large, prehensile upper lip, typical of the present-day elk, was absent in *C. gallicus*, which probably had a simple rhinarium like other cervids.

The maxillae are also largely retouched: the caudal extremity is directly connected to the plaster bridge, the suborbital opening and zygomatic processes are not preserved, the alveolar portion is covered by plaster.

Azzaroli (1952) hypothesised the presence of upper canines. Indeed, the lower edge of the right maxillo-premaxillary suture, in lateral view, curves downwards and, in palatal view, widens, leaving space for the alveolus of the tooth. Unfortunately, in this case too, it is not clear if this morphology is the work of restorers.

What is more, on the right maxilla, in front of P^2, there is an alveolar structure that leads one to suppose the presence of another premolar. There are doubts about the originality of this morphology too, but in its middle, embedded in the plaster, there is an enamel knob. The presence of a vestigial P^1 would be a really rare character.

Portions of the two heavily damaged mandibles are present, united by two metallic bridges. Mandibular symphysis and ascending branches have been rebuilt approximately, without incisor alveoli, chin-rest forum, mandibular condyles and angular processes.

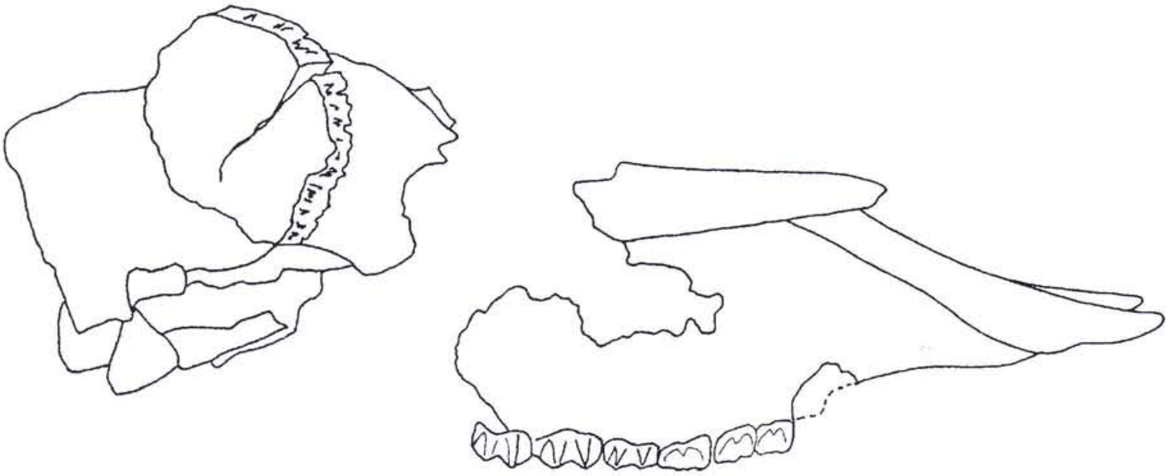

Fig. 1 - *C. gallicus*, Sénèze. Typus, skull, lateral view (1/3)-. After Azzaroli, 1952, pl. 15, fig. 1 modified.

Teeth

Both in the mandible and in the upper jaw, the right tooth rows are better preserved, showing all the jugal teeth in a different state. The teeth are very worn, which denotes an advanced age, in line with the large development of the antlers and the complete ossification of bones.

Teeth confirm the attribution to the Alcini Tribe due to: the typically short crowns which are swollen at their base; the convergence between lingual and labial walls; the tilted position of single lobes with regard to the axis of teeth row (mesostyle and parastyle project labially in the upper row, mesostylid and entostylid project lingually in the lower row); the pronounced molarisation of lower premolars; the typical morphology of P_4 with the hypoconid totally separated from the labial wall; and the well developed third lobe of M_3. Besides characters which are typical of the tribe, other peculiar morphologies place this specimen apart from more recent elks.

All these characters are described below, with reference to Heintz (1970) for both nomenclature and interpretation of lower premolar evolution.

Lower tooth row: The three left premolars are absent.

In the right jaw, P_2 preserves the only hypoconid. P_3 shows a well-developed entoconid, backwardly elongated. Paraconid and metaconid are bounded together, resulting in a closed lingual wall that forms a median fossa with a little enamel island. The general structure is the same as in present-day elk and corresponds to the fourth stage of the molarisation process of lower premolars described by Heintz (1970).

P_4 lacks the entoconid and shows the typical morphology of the tribe with a well-developed hypoconid separated from the labial wall. In labial view, under the paint, it is possible to see a bulge between hypoconid and protoconid. By comparison with Forest Bed remains, this bulge would appear to be a small ectostylid. The protoconid, in occlusal view, shows a little pinch, directed backwards, on its labial side.

All the molars show a large ectostylid and the two lobes are strongly tilted with regard to the tooth row axis, with metastylids and entostylids projecting labially. A *Paleomeryx* fold (discussed below) is not present in any of them.

Upper tooth row: Premolar dimensions increase from P^2 to P^4, while in cervids, usually, P^2 is longer and P^4 is mesio-distally compressed, with a greater superposition of the cones of the two lobes simulating a half molar (Heintz 1970).

P^3 and P^4 (P^2 lacks the whole lingual wall) show a little lingual cingulum. P^4 has a well-developed parastyle, labially elongated, and a little enamel island in the central fossa.

The molars show well-developed parastyle and mesostyle, in particular the parastyle of M^3 extends labially and bends slightly backwards. M^2 and M^3 (M^1 lacks the lingual surface) have, lingually, between the two lobes, a large entostyle with cingulum. An extremely developed protoconal fold, typical of upper molars of Villafranchian cervids, is present on M^3. It is not known if this fold was present on the other molars, their protocone being absent (discussion is referred in a following chapter).

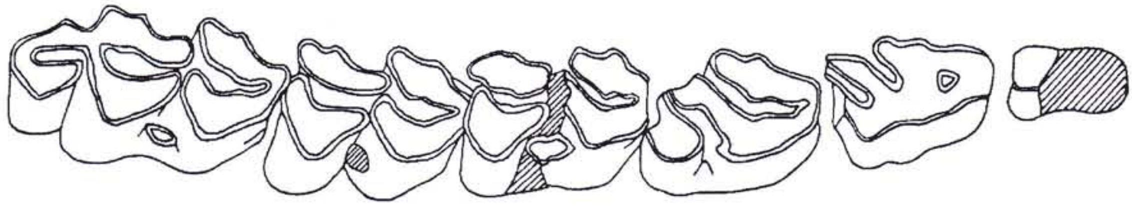

Fig. 2 - *C. gallicus*, Sénèze. Typus, lower tooth row, occlusal view (1/1). After Azzaroli, 1952, fig. 2 modified.

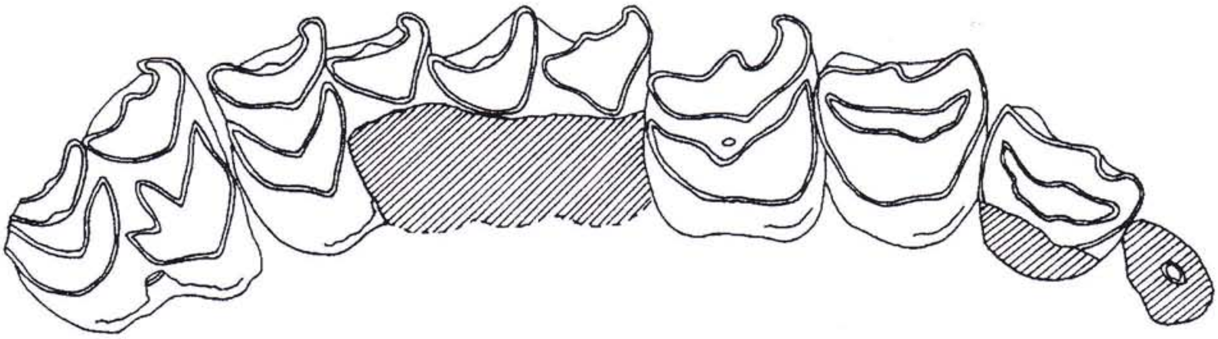

Fig. 3 - *C. gallicus*, Sénèze. Typus, upper tooth row, occlusal view (1/1).

Axial skeleton

The axial skeleton consists of numerous rib fragments and a practically complete spine. Cervical vertebrae are well spaced from one another, increasing the length of the neck, and are lined up on a nearly vertical axis, giving to the head a more cervine than alcine position. Thoracic and lumbar vertebrae preserve fragments of spinosus and transverse processes. This fact, together with the mistaken assembly of the whole skeleton, makes it difficult to estimate the stature of the animal.

What is more, some vertebrae do not belong to the same specimen, because the articular surfaces of vertebral bodies are not healed, indicating a young age in contrast with the more advanced one attested by the worn teeth and bone morphology in general. Sacral vertebrae, healed together, are heavily repaired. Caudal vertebrae are absent.

Limb skeleton

All long bones are slender, but do not show the thinning of diaphysis with regard to epiphysis pronounced as in *A. alces.* As for teeth, the variability in the epiphyseal morphology between *Alces* and *Cervalces* is very low and does not encompass the individual variability. In this respect the Tribe Alcini is very conservative in postcranial morphology. Ossification is advanced, with the complete fusion of all the bony elements. For morphometrical data see Breda (2001).

Pelvic and scapular girdles: The left scapula consists of the only proximal portion (glenoid cavity and neck); the right one preserves a good part of the fossa supra and subspinate, but lacks their cranial and caudal edges. The pelvis is more or less complete but heavily deformed.

Zeugopodius and stylopodius: The proximal epiphysis of the left humerus (the right one is absent) is larger than in present-day elk, probably in relation to the greater weight that the shoulders had to bear due to the wider antlers. The distal epiphysis shows a large cavity on the lateral surface of the trochlea, and the lateral condyle is smaller than in *A. alces.*

The two radii show an adult age, considering the total fusion of the distal epiphysis of ulna. The ulnae diaphysis is almost completely missing and the articular facets to the radius are badly damaged. The olecranons are in a good state and larger than in present-day elk.

Femurs and tibias, both in a good state, show all typical characters of *Alces*. The presence of the proximal extremity of the tibial crest, generally poorly mineralised, once more confirms advanced age.

Carpal and tarsal bones: The right pisiform, small cuneiforms, the left malleolus and the distal articular portion of the left calcaneus are absent.

Azzaroli (1952) reports, as already mentioned by Scott (1885), that the fusion among tarsal elements in the American *Cervalces scotti* is more advanced than in other Cervids, with the large cuneiform sometimes joined to the metatarsus, and confirms this character for some present-day specimens. Pavlow (1906) described a fossil specimen of *A. alces* with the three cuneiforms joined to the cubonavicular. In the specimen from Sénèze, the left cubonavicular is perfectly joined to the large cuneiform and the suture line is not visible; the right one is free.

The other bones do not present any specific character.

Metapodials: The right metacarpus is in a good state and its length is a little longer, in comparison with the other bones, than in present-day elk's (Heintz 1970; Geist 1999). The greater length of the left metacarpus is due to a wrong restoration of the diaphysis that produces also torsion between the two epiphysis.

On the lateral posterior surface of the right metatarsus, and to a lesser degree of the left, a prominence descends from the proximal epiphysis along the first part of the diaphysis. This structure, not found in *A. alces*, but present in some Bovids, could be a rudiment of a lateral metatarsus (of the fifth digit) fused to the cannon bone. What is curious, though not interesting for identification, is the presence of an exostosis on the median surface of left diaphysis, probably indicating a hard blow.

Two telemetacarpals, with distal epiphysis and a portion of diaphysis, are present. In lateral view, the diaphysis posterior edge is more posteriorly developed than in present-day elk.

Phalanges: There are all the 24 principal phalanges, numerous lateral phalanges and three big sesamoids.

First and second phalanges show the typical slender shape of Alcini but with diaphysis less thin than in present-day elk.

The third phalanx is typically elongated with the characteristic shape of proximal facets. The abassial facet shows a dorsal process that protrudes medially, over the assial facet, rising along the posterior edge of the pyramidal prominence. This character should be typical of the tribe because it is present both in *A. alces* and in *C. latifrons* (Chaix & Desse, 1981; Pfeiffer 1999a).

Cranial characters of *C. gallicus* and *C. latifrons*

Cervalces specimens, as fossil *A. alces*, usually preserve only the neurocranial portion, with occipital, parietals, temporals and frontals up to the upper edge of the orbit. The specimen from Sénèze is more complete but in a poor state of preservation, so it was possible to verify in it the presence of some characters only of *Cervalces* cranial morphology.

The pedicles show a generally circular section in *Alces* and an elliptical one, with a smaller dorsoventral diameter, in *Cervalces* (Fig. 4). The rate between longer and shorter diameters is about 85:100 in specimens from Mosbach and 81:100 in those from the Forest Bed Formation. In *C. gallicus* the difference between the two diameters is less than in *C. latifrons* in which the inferior surface of the pedicle base is constricted to allow the movement of the coronoid process of lower jaw. The burr is oblique in *Cervalces*, with the superior edge more medially located (Pfeiffer 1999), and nearly vertical in *Alces*.

C. latifrons, in comparison with *C. gallicus*, shows a greater development of all the muscular insertion sur-

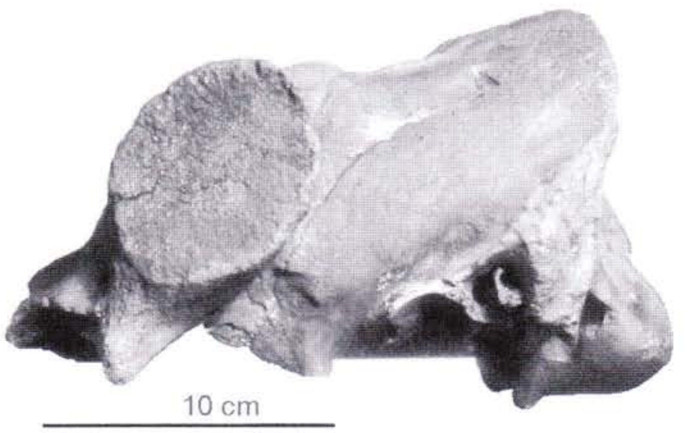

Fig. 4 - *C. latifrons*, Gimbsheim. NHM 1979/10, skull, lateral view, showing the elliptical outline of the pedicle.

faces and of the bony sutures, all characters depending, at least partially, on the sex and the age of the animal. The structural adaptation, made necessary by an increase in size, takes place almost in the same way, both during individual onthogeny and along a phyletic line gradually increasing in size. The discriminant value of these features is, in this way, restricted. For example, the nuchal crest and the mastoid processes are more developed in *C. latifrons*, so the occipital is proportionately larger with a lightly concave squama between condyles and nuchal crest. In the same way *C. latifrons* shows stronger supraoccipital and supratemporal crests with two distinct knobs: on the suture line between frontals and parietals (Azzaroli 1953) and, sometimes, on their more medial edge, halfway between the first knob and the supraoccipital crest.

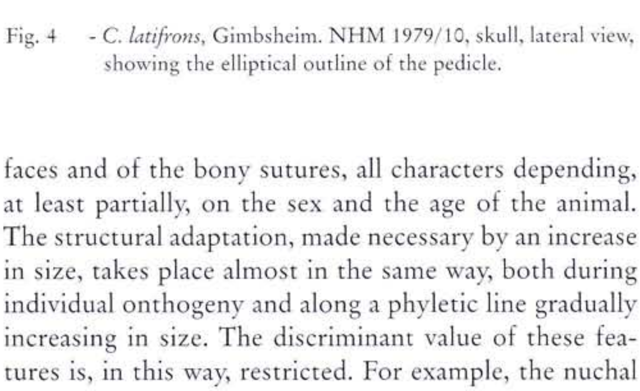

Fig. 5 - Condiles and occipital opening, occipital view (1/3): A) *C. latifrons*; B) *C. gallicus*.

Pfeiffer (1999b) suggests that in *C. latifrons* the frontals, between pedicles, are reinforced in their transverse section, building a bony bridge to balance the big lateral extension of antlers. This feature is present in two skulls (NHM 1979/10 and coll. Menger 1521) examined by Pfeiffer (1999b, fig. 7b and 8b) and on some other specimens (for example NHM 1944/240 and IQW 1965/3409), but the big part of *C. latifrons* skulls from Germany, and all the English specimens, lack this morphology (Breda 2001).

The occipital condyles are more laterally elongated in *C. latifrons*, more narrow and protruding from the occipital squama in *C. gallicus*. The greater size of the condyles of *C. latifrons* is related to the greater weight of the skull, and their morphology (more similar to that of *A. alces*) would suggest a more horizontal set of the head.

In *C. gallicus* from English Forest Bed (specimen M46108 from Dogger Bank and M6101 from East Runton), the occipital foramen shows, on the upper edge, a nuchal tubercle (not visible in the specimen from Sénèze because broken) and it is generally rounded in shape. On the contrary, in *C. latifrons* the upper edge of the occipital foramen lacks the nuchal tubercle, is nearly straight and bends sharply at the two lateral edges that go down almost parallel. The foramen presents, in this way, a general square shape (Fig. 5).

As regards the facial skull of *Cervalces*, Pfeiffer (1999b) suggests that *C. gallicus* and *A. alces*, in comparison with *C. latifrons*, have a longer and lower viscerocranium. To date, only one facial skull of *C. gallicus* (the Sénèze specimen) and one of *C. latifrons* (IQW 1965/3409 from Süßenborn) have been found. The holotype of *C. gallicus* is in a bad state of preservation, lacking a big part of maxillae and all the orbital portions, so it is difficult to state about the length of its viscerocranium. However, *A. alces* face is typical, among deer, for its bulging profile, inflated at the level of the nasals (Sher 1987) and not lower than *C. latifrons* viscerocranium.

The Süßenborn specimen lacks the premaxillae but their connection to the nasals should have been approximately the same as in *C. gallicus*, so the reconstruction by Sher (1987, fig.1) is here confirmed. Kahlke's statement (1990), that the connection between nasals and premaxillae was "distinctly smaller" than in *C. gallicus* and *C. scotti*, is not supported by personal observations. Kahlke (1990, page 86) asserts: "The distance between the distal part of the os maxillare and the isolated part of the os nasal is approximately 15-20 mm", but the premaxillae extend more backward than the maxillae anterior edge, covering it (the suture surface is evident on the maxillae). So we have to add 15 mm, of superposition along the nasals, to the measure taken by Kahlke.

Dental characters of the genus *Cervalces*

From the analysis of the specimen from Sénèze and of the numerous jaws from the Forest Bed and from many German localities (Untermassfeld, Süßenborn, Voigtstedt, Mosbach, Mauer), it is possible to summarise the dental characters of *Cervalces* in comparison with those of *Alces*. The morphologies common to all the Alcini, detailed above, are here omitted.

The length of upper and lower grinding tooth rows is less in *C. gallicus*, intermediate in *A. alces* and greater in *C. latifrons*. The ratio between premolar and molar row lengths lies in the same range for the three species. For morphometrical data see Breda (2001).

The hypothesis of a gradual molarization of P_3, by closure of the lingual wall, in the evolution from *C. gallicus* to *C. latifrons* (Mauser 1990), is not confirmed here, the P_3 of the holotype showing the parastylid connected to the metastylid.

A cingulum is frequently present on the anterior edge of the lower molars and of P_4; it could correspond to the anterior fold described by Heintz (1970) for Villafranchian Cervids and interpreted as a vestige of the first lobe.

A well-developed ectostylid between the two labial lobes of lower molars is always present both in *C. gallicus* and in *C. latifrons*. The ectostylid is present even in several specimens of *A. alces* but is smaller and occurs, sometimes, only in M_1. An analogous accessorial tubercle is present, between second lobe and talonid of M_3, in some *Cervalces* specimens, or, still more reduced, in P_4 between hypoconid and labial wall.

On the lingual side of the upper molars of the specimen from Sénèze, an entostyle, with a cingulum, is present. This entostyle appears to have the same functional purpose as the ectostylid and it is a very variable feature, being sometimes present also in *C. latifrons, A. alces, Megaloceros* and *Cervus*.

In the upper teeth of *Cervalces*, the mesostyle and parastyle are more developed and more labially and posteriorly bent than in present-day elk.

The observed wrinkled feature of the surfaces of the crowns, typical of *Megaloceros*, is sometimes observed also in the Alcini, in particular on the lingual wall of the upper teeth and on the labial wall of lower ones. This character is probably more frequent in *Cervalces* than in *Alces*; it is, however, very variable.

Protoconal fold and *Paleomeryx* fold are worth a separate discussion.

Protoconal fold is defined as an enamel fold, englobing dentine, emerging from the lingual side of the posterior edge of the protocone and oriented almost antero-posteriorly (Heintz, 1970). This fold is always present on the upper molars of Villafranchian Cervids and its development varies according to wear (in very worn teeth it is reduced to a simple irregularity of the posterior wing of the protocone); to the order number of the tooth (reduced on M^1 and more developed on M^3); to the geological age of the species (well developed in species from the old Villafranchian and then progressively less); and to the species size (geological age being equal, it is more developed in small or middle size species).

Paleomeryx fold is another enamel fold, englobing dentine, situated on the labial side of the posterior edge of the protoconid of the lower molars. It was identified for the first time in a Miocene ruminant, from which it takes its name. It is present both in cervids and in Giraffoidea, but is missing in bovids of any geological age. Among Cervids it is usually present in the Miocene, sporadic in the Pliocene and was never observed in the Villafranchian (Heintz 1970).

Both these folds could be construed as structures reinforcing the tooth and their evolution seems to be homologous (Heintz 1970). It is possible that the formation of Protoconal and *Paleomeryx* fold preceded (phylogenetically) the formation of the posterior wings, respectively, of Protocone and Protoconid. At an early stage these wings did not exist and their function was carried out by the respective "folds". Then, as the posterior wings developed, the "folds" gradually shrank and finally disappeared (Heintz 1970).

Azzaroli (1952), in his description of *C. (L.) gallicus*, speaks about "traces of *Paleomeryx* fold in M_1, eventually in M_2" and specifies "it is not a real fold, but a clear groove, little deep, obliquely directed from the top downwards and backwards".

On the validity of this character, a heated debate, which is still in progress, broke out, involving nomenclatural and taxonomical problems. Azzaroli (1979, 1982, 1985) gave no great diagnostic value to this morphology, whereas Heintz & Poplin (1981) considered it a determining factor for the genus. Again lacking a real *Paleomeryx* fold (it is rather a "pincement") the same character defining the genus *Cervalces (Libralces)* is missing, and so, for the French authors, the genus has no reason to exist. These authors attribute the specimens of *C. gallicus* to *Alces*. In this work traces of *Paleomeryx* fold were not observed on the molars. We agree with Azzaroli (1979, 1982, 1985) that this character does not have a determining value in the description of the genus *Cervalces*, which is centred mainly on the cranial structure.

More acceptable from a chronologic-evolutionary point of view, is, on the contrary, the presence of a well-developed protoconal fold on upper molars. It is present on the M^3 of the holotype from Sénèze (the protocones of M^1 and M^2 are missing), on all the upper molars of German specimens (remains from the English Forest Bed lack upper molars) and of living and fossil *A. alces.* Sometimes there is a similar structure on upper premolars. This feature is present in Alcinae and North American cervids but not in European ones (Geraads, 1983).

As wearing proceeds, protoconal fold and posterior wing of the protocone merge together to form a little central enamel hollow that will disappear in the very worn teeth. On the presence of this character, both in premolars and in the first lobe of molars, Geraads (1983) hypothesises that upper premolars are homologous to the first lobe of upper molars.

Moreover, a little enamel fold is present on the hypocone of upper molars both of *Cervalces* and of *A. alces*. This structure, called "éperon" by Heintz (1970), is present in many living Euroasiatic deer and does not seem to be of any diagnostic value.

Taxonomic and Phylogenetic accounts of Alcinae

Alcinae Jerdon, 1874 are a cervid subfamily that shares telemetacarpal structure with Capreolinae, Rangiferinae and Oidocoileinae from the New World. They separated from other deer, probably, in the Late Miocene (Kahlke 1990) but to date remains older than the Late Pliocene, belonging to *Cervalces* lineage, have not been found. *Pseudalces mirandus* Flerov, 1962 has been described on a fragmentary male skull from the Lower Villafranchian of Stavrpol (Northern Caucasus) and its attribution is still debated. Heintz & Poplin (1981) consider it the oldest representative of the *Eucladoceros* group; Vislobokova (1986) refers this finding to the elk s. l. but recognises that it is not an ancestor of *Cervalces* and *Alces* for some more progressive features in cranial morphology.

The only living species is *Alces alces* (Linnaeus, 1758) but other fossil forms exist from the Upper Pliocene and Pleistocene of Eurasia and North America. There is no agreement among authors regarding their taxonomy and their phylogenetic relationship.

In the more traditional view, the history of Alcinae is described as a chronocline with a gradual modelling of antlers, due to the progressive shortening of beams, leading from *C. (L.) gallicus* in the Lower Pleistocene to *C. (L.) latifrons* in the Middle Pleistocene and finally to present *A. alces*. Variations in antler morphology were caused by different adaptive pressure in the two main evolutionary steps (Lister 1987, 1993b). In the transformation from *C. gallicus* to *C. latifrons*, the great increase in body size was not followed by an isometric growth of antlers, which would be disadvantageous for biomechanical reasons and from the point of view of energy expenditure. The reduction in body size from *C. latifrons* to *A. alces* alone is not enough, to justify the extreme reduction of antler span, which can be put down to environmental factors as well: the transformation from an open steppe-like environment, in which big demonstrative structures would be an advantage in sexual selection, to a coniferous forest habitat, in which these organs would impede movement (Lister 1987, 1993b).

Heintz & Poplin (1981) describe the species *Alces carnutorum* (Laugel, 1862) from the early Middle Pleistocene, as transitional, in age and size, between *C. gallicus* and *C. latifrons*. Kahlke (1990, 1997) accepts this new species, whereas Geraads (1983), Sher (1987), Vislobokova (1986) and Pfeiffer (1999) do not. Azzaroli (1982, 1985, 1994) reports the fact and puts the species in the genus *Cervalces*, without considerations concerning its validity. The remains of *C. carnutorum* are still scanty, so its taxonomical position is unclear. It is better to wait for the finding of cranial elements before choosing whether to keep it in a third species or to consider it as subspecies of *C. gallicus* or *C. latifrons*.

Besides the validity of each single species and their relationship, their split between the genus *Alces* (Gray, 1821), *Cervalces* Scott, 1885 and *Libralces* Azzaroli, 1952 is even more controversial. The difficulty in reaching agreement is primarily justified by the diverging opinion about which characters should hold a determining value (as stated above about *Paleomeryx* fold). At present, many authors recognise the only genus *Alces* (Heintz & Poplin 1981; Geraads 1983; Lister 1987, 1993a, 1993b, 1996; Kahlke 1990, 1995, 1997; Pfeiffer 1999b) while others put the fossil species in *Cervalces/Libralces* and the only living species in *Alces* (Azzaroli 1979, 1982, 1985, 1994; Vislobokova 1986; Sher 1987; Churcher & Pinsof 1987; Churcher 1991; Breda 2001).

The characters with stronger discriminant value are the osteological ones.

Antler morphology, which attracts the greater number of researchers, is very variable at an individual level and too irregular at a specific level, because dependent on sexual selection and so influenced by ethological and ecological changes. What is more, the same morphology can develop, at the same time, in more lineages leading to interpretative mistakes.

Dental morphology is a very constant character among Alcinae; in fact, the few interspecific differences do not greatly exceed the intraspecific ones. Moreover, their evolution is more dependent on dietary changes (ecological factors again) than on phylogenetic relationship.

Osteological characters, particularly cranial ones, are here considered more conservative, and it is possible to base considerations on them for taxonomic and cladistic analyses.

The present-day species, *A. alces*, distinguishes itself clearly from other Alcinae for some apomorphies, such as the narrow and deep occipital and the short nasals which are not articulated to the extremely long premaxillae.

If a gradual change between two forms, in both size and morphology, hardly justifies their division into two distinct species, a sharper variation, without superimposition of the dimensional and morphological range of the two forms, will involve their attribution to different genuses. So, only the living species is here put in the genus *Alces* whereas all the fossil forms are considered in the genuses *Cervalces / Libralces*. In support of this idea, Vislobokova (1986) states that the osteological differences between *Cervalces / Libralces* and *Alces* show the same degree of divergence as those between genuses belonging to the same tribe (es. *Cervus* and *Axis*).

Libralces and *Cervalces* are characterised, as stated above, by the same cranial characters (occipital and facial region) that distinguish them from *Alces*. The only difference would appear to be a more complicated palmature in *Cervalces*, which is not enough to maintain two genuses. For this reason Azzaroli (1982) downgrades *Libralces* to a subgenus of *Cervalces*. Churcher & Pinsof (1987) and Sher (1987) agree, Vislobokova (1986) does not, maintaining that it is better to wait for new osteological data of the American form before taking a position.

As far as regards the phylogenetic relationship between Pleistocene Alcinae, all the authors agree in considering *C. latifrons* as descending from *C. gallicus* with the eventual intermediary *C. carnutorum*. Moreover, Heintz & Poplin (1981) assert a descent of *A. alces* from *C. latifrons* by the subspecies *C. latifrons postremus* Vangenheim & Flerow, 1965 by a gradual dwarfing and shortening of the beams. *C. latifrons postremus* was signalised (Kahlke, 1975, 1976; Koenigswald & Menger, 1997) from the upper Middle Pleistocene of central Europe (Ehringsdorf, Taubach and Groß-Rohrheim), but Pfeiffer (1999b) shows that there is no morphological or metrical distinction in *C. latifrons* remains from Middle Pleistocene and suggests that antlers attributed to *C. l. postremus* belong to young specimens of *C. latifrons*. What is more, this hypothetical subspecies lacks cranial elements, so its taxonomic collocation is difficult. According to Azzaroli (1985), it survived in Siberia and Beringia during the Upper Pleistocene and reached North America to evolve into the American species *Cervalces scotti* (Lydekker, 1898). Kahlke (1990) maintains, on the contrary, that *C. scotti*, living in the territories from the East Coast to the Mississippi (Churcher & Pinsof 1987), derives from forms of the early "*latifrons*" type that crossed Beringia in the early Middle Pleistocene. Later, other populations of *C. latifrons* would reach North America at different times, but remained confined in the cold North Western Regions and retained a greater size than *C. scotti*. To these forms are referred the remains previously determined as *Cervalces borealis* Bensley, 1913, *Cervalces roosvelti* Hay, 1913 and *Cervalces alaskensis* Frick, 1937 (Churcher & Pinsof 1987).

As regards the species *A. alces*, one of its possible ancestors is *Alces brevirostris* Kretzoi, 1969 from the Middle Pleistocene of Eastern Europe, that shows a similar facial skull with nasals one-and-a-half times as long as those of living specimens and very short premaxillae (Janossy 1969). Unfortunately, description of the occipital portion is totally missing (the whole skull was destroyed, together with the jaw and antlers, in a fire) and so it is impossible to infer its taxonomic position. *A. brevirostris* was a small sized elk, with very short and strong metapodials, short neck, short beams and wide palmation, separated in the anterior and posterior portion (Vörös 1985).

It is difficult to find a place in the phylogenetic tree of Alcinae for some small sized elks from the Middle Pleistocene of Germany. Soergel (1912, 1914) observed a difference between the big specimens from Süssenborn and Mosbach p. p., with long beams (typical *C. latifrons*), associated with an open environment fauna, and the smaller specimens from Mauer and Mosbach p. p., with shorter beams, associated with a woodland fauna. Schmidt (1930) attributed a specimen from Bilshausen to the woodland form and Wernert (1957) identifies it in Hangenbieten (Alsace), but, unfortunately, nothing is known about its occipital region. Kahlke (1990) confirms the existence of two forms of *C. latifrons* and hypothesises that the smaller one, that he calls interglacial, could be the ancestor of *A. alces*. The possibility of putting this smaller sized form in a different subspecies is considered here. We have to wait for neurocranic remains to be found, to decide whether to keep it in *C. latifrons* (as Kahlke did) or put it in *A. alces*.

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REFERENCES

Azzaroli A. (1952) - L'alce a Sénèze. *Paleontogr.* It., 47: 133-141, 15-16 pls., Pisa.

Azzaroli A. (1953) - The Deer of the Weybourn Crag and Forest Bed of Norfolk. *Bull. British Mus. (Nat. Hist.), Geology*, 2 (1): 1-96, London.

Azzaroli A. (1979) - On the occurrence of the Cervid genus *Libralces* in the Pleistocene of Italy. *Palaeontogr. It.*, 71: 48-54, 21-22 pls., Pisa.

Azzaroli A. (1982) - On the Quaternary and recent cervid genera *Alces, Cervalces, Libralces. Boll. Soc. Paleont. Ital.*, 20 (2): 147-154, 1 pl., Modena.

Azzaroli A. (1985) - Taxonomy of Quaternary Alcini (Cervidae, Mammalia). *Acta Zool. Fennica*, 170: 179-180, Helsinky.

Azzaroli A. (1994) - Forest Bed elks and giant deer revisited. *Zool. Journ. Linn. Society*, 112: 119-133, London.

Azzaroli A., De Giuli C., Ficcarelli C. & Torre D. (1988) - Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 66: 77-100, Amsterdam.

Barone R. (1980) - Anatomia Comparata dei Mammiferi Domestici. V. of 644 pp., Officine Grafiche Calderini, Ed. Agricole, Bologna, Roma, Milano.

Breda M. (2001) - Gli Alcini fossili dell'Europa Nord Occidentale e i loro rapporti filogenetici. *Tesi di Dottorato in Scienze della Terra XIV ciclo*, Università di Padova, Anno Acc. 2000-2001.

Chaix L. & Desse J. (1981) - Contribution à la connaissance de l'Elan (*Alces alces*, L.) postglaciaire du Jura et du Plateau suisse. *Quartär, Jb. Erforsh. Eisziet und Steinzeit.*, 31/32: 139-190, Bonn.

Churcher C. S. & Pinsof D. (1987) - Variation in the antler of North American *Cervalces* (Mammalia; Cervidae): review of new and previously recorded specimens. J. *Vertebrate Paleont.*, 7 (4): 373-397, Washington.

Churcher C. S. (1991) - The status of *Giraffa nebrascensis*, the synonymies of *Cervalces* and *Cervus*, and additional records of *Cervalces scotti. J. Vertebrate Paleont.*, 11 (3): 391-397, Washington.

Geist V. (1999) - Deer of the World. V. of 421 pp. Stackpole Books, USA.

Geraads D. (1983) - Artiodactyles (Mammalia) du Pléistocène Moyen de Verganne (Doubs). *Ann. sci. Univ. Besançon, Geol.*, 5: 67-81, Besancon.

Heintz E. (1970) - Les cervidés villafranchiens de France et d'Espagne. *Mém. Mus. Nat. d'Histoire Nat.*, N. S., serie C, Sciences de la Terre, 22: 303 pp., Paris.

Heintz E. & Poplin F. (1981) - *Alces carnutorum* (Laugel, 1862) du Pléistocène de Saint-Prest (France). Systématique et évolution des Alcinés (Cervidae, Mammalia). *Quartärpaläontologie*, 4 (1981): 105-122, Berlin.

Janossy D. (1969), Stratigraphische Auswertung der europäischen mittelpleistozänen Wirbeltierfauna, teil 2: *Ber. dt. Ges. geol. Wiss.* A, 14 (5): 573-643, Berlin.

Kahlke H. D. (1975) - Die Cerviden-Reste aus den Travertinen von Weimar-Ehringsdorf. (III° Internat. Palaont. Kolloq.) *Abh. Zentr. Geol. Inst. Paläontol.*, 23: 201-249, Berlin.

Kahlke H. D. (1976) - Die Cerviden-Reste aus den Travertinen von Taubach. *Quartärpaläontologie*, 2: 209-223, Berlin.

Kahlke H. D. (1990) - On the Evolution, Distribution and Taxonomy of Fossil Elk/Moose. *Quartärpaläontologie*, 8: 83-106, Berlin.

Kahlke H. D. (1995) - Ein fossiler Elch aus dem Unterpleistozän von Untermassfeld in Thüringen (Mitteldeut.). *Quartär*, 45/46: 227-235, Bonn.

Kahlke H. D. (1997) - Die Cerviden-Reste aus dem Unterpleistozän von Untermassfeld. Monographien Das Pleistozän von Untermassfeld bei Meiningen (Thüringen). *Römisch-germanisches Zentralmuseum*, teil I: 184-195, Bonn.

Koenigswald W. v. & Menger F. (1997) -Mögliches Auftreten von *Trogontherium cuvieri* und *Alces latifrons* im letzten Interglazial der nördlichen Oberrheinebene. Cranium Jrg., 14 (1): 2-10, Utrecht.

Lister A. M. (1987) - Diversity and evolution of antler form in Quaternary deer. In: Wemmer, C. M. (ed.)- Biology and Management of the Cervidae. *Smithsonian Institution*: 81-98, Washington.

Lister A. M. (1993a) - The stratigraphical significance of deer in the Cromer Forest-Bed Formation. *Journal of Quaternary Science*, 8 (2): 95-108, Chichester.

Lister A. M. (1993b) - Evolution of mammoths and moose: the Holoartic perspective. In Martin, R. A. & Barnosky, A. D. (eds.) - Morphological Change in Quaternary Mammals of North America: *Cambridge University Press*: 178-204, New York.

Lister A. M. (1996) - The stratigraphical interpretation of large mammal remains from the Cromer Forest- bed Formation. In: Turner C. (ed.)- The Early Middle Pleistocene in Europe. *Balkema*: 25-44, Rotterdam.

Mauser M. (1990) - *Alces latifrons* (JOHNSON, 1874) (Mammalia, Cervidae) von der altpleistozänen Säugetier-Fundstelle Würzburg-Schalksberg (Unterfranken, BRD). *Quartäpaläontologie*, 8: 205-214, Berlin.

Pavlow M. (1906) - Études sur l'hìstorie paléontologique des Ongulés, IX. Sélénodontes posttertiaires de la Russie. *Mem. Acad. Sci. St-Pétersb.*, 20: 1-95, 1-8 pls., St. Petersburg.

Pfeiffer T. (1999a) - The Morphological distinction of Limb Bones of *Alces latifrons* (Johnson 1874) and *Megalocerus giganteus* (Blumenbach 1799) from Middle and Late Pleistocene Localities of Germany. *Kaupia. Darmstädter Beiträge zur Naturgeschichte*, 9: 113-126, Darmstädt.

Pfeiffer T. (1999b) - *Alces latifrons* (Johnson 1874) (Cervidae, Mammalia) from Late Pleistocene sediments of the Upper Rhine Valley (West Germany). *N. Jb. Paläont. Abh.*, 211: 291-327, Stuttgart.

Roman F. & Dareste de la Chavanne J. (1931) - Sur la présence d'un elan (*Alces latifrons Johns.*) dans le Pliocène superieur de Sénèze (Haute Loire). C. R. *Acad. Sciences Paris*, 192 (18): 1256-1257, Paris.

Schmidt H. (1930) - Ein skelett von *Alces latifrons* aus der Gegend von Göttingen. *Paläont. Z.*, 12: 135, Berlin.

Scott W. B. (1885) - *Cervalces americanus*, a fossil Moose, or Elk, from the Quaternary of New Jersey. *Proc. Acad. Nat. Sci. Philadelphia*, 37: 181-202, Philadelphia.

Sher A. V. (1987) - History and evolution of moose in the USSR. *Swedish Wildlife Research Supplement*, 1: 71-97, Stockholm.

Soergel W. (1912) - Das Aussterben diluvialer Säugetiere und die Jagd des diluvialen Menschen. 81 pp., Jena.

Soergel W. (1914) - Die diluvialen Säugetiere Badens. I. Älteres und mittleres Diluvium. *Mitt. grossherzgl. bad. geol. Landesants*, 9: 1-254, Heidelberg.

Thouveny N. & Bonifay E. (1984) - New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. *Nature*, 308 (5957): 355-358, London.

Vislobokova I. A. (1986) - Elks in the Pliocene of USSR. *Quartärpaläontologie*, 6: 236-242, Berlin.

Vörös I. (1985) - *Alces brevirostris* Kretzoi from the Ördöglyuk Cave at Solimar (Hungary). *Fragm. Mineral. et Palaeont.*, 12: 59-66, Budapest.

Wernert P. (1957) - Stratigraphie, paléontologie et préhistorique des sediments quaternaires d'Alsace, Achenheim. *Mém. Serv. Carte géol. Alsace-Lorraine*, 14: 254 pp., Strasbourg.