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Assessing astragalar morphology and biomechanics in western Palaearctic *Bison* populations with geometric morphometrics

Essai d'évaluation de la morphologie et de la biomécanique astragalienne des populations de bisons du Paléarctique occidental par morphométrie géométrique

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ABSTRACT

Having arrived 1.8 Ma ago, bison prevailed in the bovid assemblages of the European subcontinent for more than 1.5 Ma. The current geometric morphometric study outlines a framework of ecomorphological differences among several *Bison* populations of the western Palaearctic, shown by inferences from the tibial and tarsal joint surfaces of their astragalus. Given the principal biomechanical role of this element in the locomotion mechanism, its anatomical features could be linked to diverse functional aspects. In terms of morphological affinity, it is possible to attribute the studied fossil *Bison* astragalar material to several morphological trends. Shape variation is not explained by size differences and is possibly associated with an open-close habitat gradient, as indicated by the presence of expanded or compressed astragali, respectively. This intragroup spatial and temporal phenotypic diversity among the examined populations could indicate a biogeographic segregation influenced by regional climatic and landscape heterogeneity in the European territory during Pleistocene. Furthermore, a relation to habitat-specific locomotor ecology could be supported, revealing forms with increased cursoriality, operating in open biomes and closed-country dwellers as well.

Mots clés :
Bison
Pléistocène
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Astragale

RÉSUMÉ

Apparu il y a 1,8 Ma, le bison a régné dans les assemblages bovins du sous-continent Européen pendant plus de 1,5 Ma. La présente étude morphométrique géométrique propose un cadre de différences écomorphologiques entre plusieurs populations de *Bison* du Paléarctique occidental, révélées par les inférences des surfaces tibiales et tarsiennes de leur astragale. Compte tenu du rôle biomécanique principal de cet élément dans le mécanisme de locomotion, ses caractéristiques anatomiques pourraient être liées à divers aspects fonctionnels. En termes d'affinité morphologique, il est possible d'attribuer plusieurs tendances aux astragales fossiles des *Bisons* étudiés. La variation de forme n'est pas expliquée par une différence de taille et pourrait être associée à un gradient d'habitats ouverts à fermés,

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comme l'indique la présence d'astragales respectivement étirées ou compressées. Cette diversité phénotypique spatiale et temporelle pourrait indiquer une ségrégation biogéographique, influencée par l'hétérogénéité climatique et paysagère régionale, sur le territoire européen pendant le Pléistocène. De plus, une relation avec l'écologie locomotrice propre à l'habitat pourrait être soutenue, révélant des formes ayant une cursorialité accrue, opérant aussi bien dans des biomes ouverts que dans des milieux fermés.

1. Introduction

The relatively abundant and well-preserved fossil record of bovids has repeatedly served as a valuable tool in palaeoecological studies that depend on detecting the relation between morphology and specialized function, providing an illumination of shape variation through time and space (e.g., Barr, 2014, 2015; DeGusta & Vrba, 2003; Kappelman, 1988; Klein et al., 2010; Plummer et al., 2008; Wilson & Reeder, 1993). Several representatives of the genus *Bison* in the Bovinae subfamily have been a predominant component of the Pleistocene herbivore mammal faunas, as shown from numerous fossil sites in the European subcontinent since the beginning of the Late Villafranchian (~1,8 Ma). During the 1.8–1.0 Ma interval, several early members of the genus *Bison* show a wide European distribution, being present in the northern part of the Mediterranean basin and in central, southeastern and western Europe. The first advanced bison or often called "true bison" appeared at the subsequent early/middle Pleistocene transition. The short-horned woodland wisent *Bison schoetensacki* Freudenberg 1914 is known from several German, French, British and Italian sites (Breda et al., 2010; Brugal, 1995; Kahlke et al., 2011; Moullé, 1992; Sala, 1986). It persisted until the middle Middle Pleistocene, shortly after the appearance of the larger broad horn-cored *B. priscus* Bojanus 1827. The latter taxon, often called steppe bison, survived throughout the Late Pleistocene and spread further north and across a vast geographic region of the western Palaearctic, reaching northern Eurasia and even invading mid-latitude northern America (Kahlke, 1999; Shapiro et al., 2004). A phenotypic diversity, driven by climatic fluctuations and landscape-vegetational heterogeneity, is possibly imprinted in the limb structure among primitive and more evolved forms, as previous studies have already partly shown (e.g., Maniakas and Kostopoulos, 2017). Here, a morphological framework for interpreting part of the possible spatial and temporal variation in the astragalar morphological and biomechanical features of several Western Palaearctic bison is attempted. Ecomorphological patterns, in terms of functionally related habitat signals, are investigated and visualized via the application of geometric morphometrics.

2. Material and methods

2.1. Biomechanical background of the astragalus

The skeletal postcranial element employed in this analysis is the bovid astragalus. Astragali are the most commonly preserved bones in the fossil record due to their favorable taphonomic properties (Barr, 2015), providing a quite robust statistical sample. In terms of functional morphology, this limb component is strongly involved in the locomotion mechanism and thus, its morphological properties would be linked to diverse locomotor aspects, at least to some extent, as have been suggested by some recent studies of taxon-free habitat reconstructions (Barr, 2014, 2015; DeGusta and Vrba, 2003; Plummer et al., 2008, 2015). Research on astragalar ecomorphology has been merely based on multivariate analyses of raw (e.g., DeGusta and Vrba, 2003; Plummer et al., 2008, 2015) and size-corrected measurements (e.g., Barr, 2014, 2015). This multi-levelled bone is considered as a principal part of a rather complex structure (Fig. 1a), i.e., the double-trochleated hinge joint between the metatarsus and the tibia that functions in the plantar and dorsal flexion of the foot (Barr, 2014). This complex also includes the calcaneus, the cubonavicular bone and the distal tibia, transporting the animal's weight via a "cam-like mechanism" (sensu Schaeffer, 1947) or the "four-bar linkage hock joint system" described by Alexander and Bennett (1987). The latter is involved in the motion to the anteroposterior direction across the upper ankle joint between the tibia and the astragalus and the transverse tarsal joint between the astragalus and the cubonavicular under the stabilizing action of the lower ankle joint between the astragalus and the calcaneus (Schaeffer, 1948). However, the functional role of the astragalus and its relation to habitat preference is debatable. A recent study (Klein et al., 2010) suggested that this skeletal element contributes with rather limited power in ecomophological studies, as the observed shape variation is mainly affected by differences in body size and phylogeny. Other authors (e.g., Barr, 2014, 2015), while controlling for body size, have linked its morphology to a habitat-specific locomotion under several functional hypotheses.

2.2. Studied localities and species

The studied fossil material studied, consists of 83 astragali, representing populations of various taxa of the genus *Bison* from the early, middle and late Pleistocene of southwestern, southeastern and central-northern European region (Fig. 2). Specimens of Early Pleistocene bison were obtained from three key localities, which bear fossil mammal assemblages with similar faunal characteristics. *Bison* astragalar remains, referred to *Bison* sp., were derived from the localities of Venta Micena, located at the margins of the Guadix-Baza basin in southeastern Spain (Moyà-Solà, 1987) and Apollonia, in Mygdonia basin in northern Greece (Kostopoulos, 1997). Both are dated between 1.2–1.6 Ma with Venta Micena considered slightly older than Apollonia