

THE *BISON* SAMPLE FROM THE EARLY MIDDLE PLEISTOCENE SITE OF CONTRADA MONTICELLI (APULIA, SOUTHERN ITALY)

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Abstract. Several craniodental and postcranial Bovinae fossil remains coming from the early Middle Pleistocene Contrada Monticelli (CM) site (Castellana Grotte, BA) and preserved at the Museum of Earth Sciences at the University of Bari are here studied in detail for the first time. In addition to Bovinae, the fauna of CM includes several Galerian taxa such as: *Canis mosbachensis* Soergel, 1925, *Palaeoloxodon antiquus* (Falconer & Cautley, 1847), *Stephanorhinus hundsheimensis* Toula, 1902, *Equus* sp. and *Dama* cf. *roberti* Breda & Lister, 2013. Although the scarcity of the sample and the lack of skulls, horncores or metapodial remains should suggest caution, the detailed morphological and biometric analyses allow to refer these remains to a large form of bison, here provisionally classified as *Bison* cf. *schoetensacki* Freudenberg, 1914. The presence of this species in the CM site would represent the southernmost occurrence of this taxon in Europe, validating the biochronological attribution of the CM site to the Isernia Faunal Unit (ca. 0.6 Ma). The presence of this bovid, and other large mammals in the site, provides further clues for the reconstruction of the paleoenvironment of Mediterranean Europe during the early Middle Pleistocene.

INTRODUCTION

The first bisons dispersing in Europe are grouped in the subgenus *Eobison*, which most likely

originated in Asia during the Late Pliocene and, around the end of Villafranchian biochron (ca. 1.8-1.5 Ma), reached the western Palearctic (Sorbelli et al. 2023 and reference therein). At the beginning of the Epivillafranchian, these primitive forms were replaced by larger and more derived bovids, belonging to the subgenus *Bison* (*Bison*) (Sorbelli et

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Tab. 1 - Data and related reference used in Fig. 1.

Sites	Species	Age	MIS	Reference (most recent)
Capena	<i>Bison (Eobison) cf. degiulii</i>	Early Pleistocene	?	Sorbelli et al. (2023)
Salita di Oriolo	<i>Bison (Eobison) cf. degiulii</i>	Early Pleistocene	31–28	Sorbelli et al. (2023)
Castagnone	<i>Bison</i> sp.	Early Pleistocene	31–28	Siori & Sala (2007)
Cava Redicicoli	<i>Bison cf. shoetensacki</i>	Early Pleistocene	20	Sorbelli et al. (2023)
Slivia	Bovidae indet.	Early Pleistocene	?21–19	Bon et al. (1992)
	<i>Bison cf. shoetensacki</i>			
Domegliara (=Selva Vecchia)	<i>Leptobos</i> sp., <i>Bos</i> sp.	?Early Pleistocene - early Middle Pleistocene	?	Bon et al. (1991)
Val di Chiana	<i>Bison cf. shoetensacki</i>	Early Pleistocene-Middle Pleistocene	?	Azzaroli (1984)
Cava Arnolfi	<i>Bison</i> sp.	Middle Pleistocene	17	Sala (1986)
Cesi	<i>Bison shoetensacki</i>	Middle Pleistocene	17	Sorbelli et al. (2023)
Notarchirico - Levels I2-F	Bovinae indet.	Middle Pleistocene	17	Moncel et al. (2023)
	<i>Bison shoetensacki</i>			
Notarchirico - Levels D, A, Alfa	<i>Bison shoetensacki</i>	Middle Pleistocene	16	Cassoli et al. (1999)
	<i>Bison</i> sp.			
	cf. <i>Bos primigenius</i>			
	<i>Bos primigenius</i>			
Vitinia	<i>Bison</i> sp.	Middle Pleistocene	16	Marra et al. (2014)
	Bovidae indet.			
Cava di Breccia - Casal Selce 2	Bovidae indet.	Middle Pleistocene	15	Strani et al. (2021)
Isernia La Pineta	<i>Bison shoetensacki</i>	Middle Pleistocene	15	Sala (1986)
Cengelle 1	<i>Bos</i> sp.	Middle Pleistocene	?17-15	Bon et al. (1991)
Atella	Bovinae indet.	Middle Pleistocene	13	Rocca et al. (2023)
Loreto	<i>Bison shoetensacki</i>	Middle Pleistocene	13	Sala (1986)
Visogliano	<i>Bison cf. shoetensacki</i>	Middle Pleistocene	13-11	Abbazzi et al. (2000)
Serbaro di Romagnano	<i>Bos primigenius</i>	Middle Pleistocene	13-11	Bon et al. (1991)
G.R.A. (Grande Raccordo Anulare)	<i>Bos primigenius</i>	Middle Pleistocene	13	Mecozzi et al. (2023)

the ones from Dürfort (Brugal 1995), La Vassière and Saint Prest (Brugal & Fosse 2005) in France and the ones from Slivia, Notarchirico (Caloi & Palombo 1979) and Isernia la Pineta (Sala 1986) in Italy. Until the end of the last century, the most common hypothesis designed a late dispersal of *B. shoetensacki* in Europe, dating its arrival at the beginning of Middle Pleistocene (ca. 0.8 Ma). Recent discoveries, however, predate the first occurrence of this species at the end of the Early Pleistocene, as documented in the lower layers of Cal Guardiola (Spain, 1.1-1.0 Ma) and in the roughly coeval site of Le Vallonnet (France, ca. 1.2 Ma) which represent the earliest occurrence of this species in Europe (Moullé 1992; Sorbelli et al. 2021). These remains, altogether with the slender *Bison menneri* from Untermassfeld (Germany, ca. 1.1-1.0 Ma), suggest that the first *Bison (Bison)* already appeared at the beginning of the Epivillafranchian biochron (Moullé 1992; Sher 1997; Kahlke 2007; Bellucci et al. 2015; Sorbelli et al. 2021). The abundant fossil record referable to *B. shoetensacki* suggests that this taxon was widely distributed across the whole Europe, representing the most common large bovid during the Epivillafranchian and Galerian, from ca. 1.2 to 0.6 Ma (Sorbelli et al. 2021). Around 0.6-0.5 Ma, the large *Bison prisus* Bojanus, 1827, the steppe wisent, reached the western Palearctic and rapidly dispersed in Europe, becoming the dominant large

bovid of the continent (Gromova 1935; Sala 1986; Sher 1997; Kahlke 1999). This extremely polymorphic species thrived in the vast Eurasian steppe and woodlands of the Middle and Late Pleistocene persisting until the beginning of the Holocene (Kahlke 1999; Kirilova et al. 2015; Massilani et al. 2016). At the state of the art, it is unclear if the larger *B. prisus* co-occurred with the last representatives of *B. shoetensacki* in Europe. Despite some authors claim that the latter species survived until the Late Pleistocene (Palacio et al. 2017), recent reappraisals of the *B. shoetensacki* record show that no reliable remains of this taxon are found after 0.5 Ma, thus suggesting that the overlap of the two large Bovinae could be restricted to few early Middle Pleistocene localities (e.g., Mosbach) (Grange et al. 2018; Sorbelli et al. 2021). In Italy, *B. shoetensacki* (or *B. cf. shoetensacki*) is attested in several Early and Middle Pleistocene sites (Fig. 1 and Tab. 1), however, with the exception of the extremely abundant sample from Isernia la Pineta (Sala 1986), all the referred records are quite scanty and fragmentary.

Bos primigenius Bojanus, 1827, also known as the auroch, is another large bovid, which spread in Europe during the Middle Pleistocene. Although traditionally its origins were traced back to Asia (e.g., Pilgrim 1937), the hypothesis of an African provenance has been recently formulated (Martinez-Na-

varro et al. 2007). The findings from the site of Wadi Sarrat (Tunisia, 0.7 Ma) would seem the putative earliest record of *B. primigenius* thus validating the African origins of the genus (Martinez-Navarro et al. 2014). In Europe, the most ancient record of *B. primigenius* is reported in the early Middle Pleistocene Italian sites of Venosa basin (Potenza; Caloi & Palombo 1979; Cassoli et al. 1999) and G.R.A. km 2 (Rome; Caloi & Palombo 1986). Recently *B. primigenius* has been also reported at Ponte Molle (Rome; ca. 0.5 Ma; Mecozzi et al. 2021) and Fontignano 2 (Rome; ca. 0.4 Ma; Iannucci et al. 2021). According to the latter authors, the presence of *B. primigenius* in the early Middle Pleistocene (older than Fontana Ranuccio FU) in the Italian Peninsula cannot be confirmed.

The Middle Pleistocene site of Contrada Monticelli (CM) (Castellana Grotte, Bari, Apulia, southern Italy, 40°49'50"N, 17°10'27"E), has revealed a faunal assemblage biochronologically attributed to the Galerian Mammal Age, in particular to the Isernia Faunal Unit (ca. 0.6 Ma; Mecozzi et al. 2017; Stefanelli et al. 2021, 2024). The site yielded numerous mammal species, among which *Palaeoloxodon antiquus* (Falconer & Cautley, 1847), *Stephanorhinus hundsheimensis* (Toula, 1902), *Dama cf. roberti* Breda & Lister, 2013, *Canis mosbachensis* Soergel, 1925 (Luperto Sinni & Colucci 1985; Mazza & Varola 1999; Mecozzi et al. 2017; Stefanelli et al. 2021, 2024), providing important clues on the paleoenvironmental and paleoecological context of southern Italy during the Middle Pleistocene. In the broad European geographical context, CM documents the southernmost occurrences of *C. mosbachensis* and *D. cf. roberti*.

The bovid sample of CM is represented by several cranial and postcranial remains never described. These fossils are herein studied for the first time, to refine their taxonomical assignment based on morphological and biometrical characters. The comparison with the bovine fossil material described in the literature is also performed to support the taxonomical attribution of the sample present at CM and discuss its morphological variability and biochronological/biogeographical distribution in western Europe.

MATERIAL AND METHODS

The bovid sample from the Contrada Monticelli (CM) site is housed in the Museum of Earth Science of the University of Bari, Italy. Each speci-

Catalogue specimen	Anatomical portion	Side	Age Classes
MSTB - CM 30639	Hemimandible with P ₂ -M ₃	Left	Late adolescence
MSTB - CM 30640	Mandibular fragment	Left	Late adolescence
MSTB - CM 30641	Hemimandible with P ₂ -M ₃	Left	Late adolescence
MSTB - CM 30642	Mandibular fragment	Left	Late adolescence
MSTB - CM 30643	Hemimandible with DP ₄ -M ₂	Right	Early adolescence
MSTB - CM 30644	Hemimandible with M ₃	Left	Adult
MSTB - CM 30645	Hemimaxilla with P ² -, P ³ , M ¹ -M ³	Left	Adult
MSTB - CM 30646	Hemimaxilla with M ² -M ³	Right	Adult
MSTB - CM 30647	Hemimandible with M ₂ -M ₃	Right	Adult
MSTB - CM 30648	Humerus fragment	Left	Adult
MSTB - CM 30649	Humerus fragment	Left	Adult
MSTB - CM 30650	Femur	Left	Adult
MSTB - CM 30651	Coxal bone	Right	Adult

Tab. 2 - List of *Bison cf. schoetensacki* remains from Contrada Monticelli studied in this work.

Specimen	Measurement				M ¹	M ²	M ³
Upper teeth							
MSTB - CM 30645	Length				27.6*	31.47	34.61
	Width				22.8	27.7	28.13
MSTB - CM 30646	Length					36.34	34.52
	Width					25.83	26.87
Lower teeth							
		P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
MSTB - CM 30639	Length	13.79			29.22	33.16	41.3*
	Width	9.74			14.37	15.32	14.8*
MSTB - CM 30641	Length	12.33	20.33		20.04	28.8	40.45
	Width					15.21	16.2*
MSTB - CM 30643	Length					34.04	
	Width					14.67	
MSTB - CM 30644	Length						46.25
	Width						15.57
MSTB - CM 30647	Length					35.82	40.36
	Width					14.63	14.72

Tab. 3 - Measurements in mm of *Bison cf. schoetensacki* upper and lower teeth from Contrada Monticelli (approximated measurement are marked with *).

men is marked with an identification code, which consists of an acronym MSTB - CM (Museo Scienze della Terra Bari - Contrada Monticelli) followed by a catalog number. The record consists of 7 craniodental and 4 postcranial remains, as reported in Tab. 2. The morphological descriptions of the dental and skeletal elements follow the nomenclature used in Barone (1980), Sala (1986), Gentry (1992), Sorbelli et al. (2021) and Sorbelli et al. (2023), all explained in anatomic plates in Fig. 2 and SD Fig. 1. All measurement's abbreviations used in the text are explained in Tab. 3 for craniodental remains and in SD Tab. 1 for postcranial ones. The measurements were taken with a digital caliper to the nearest 0.1 mm following the methodology by Sala

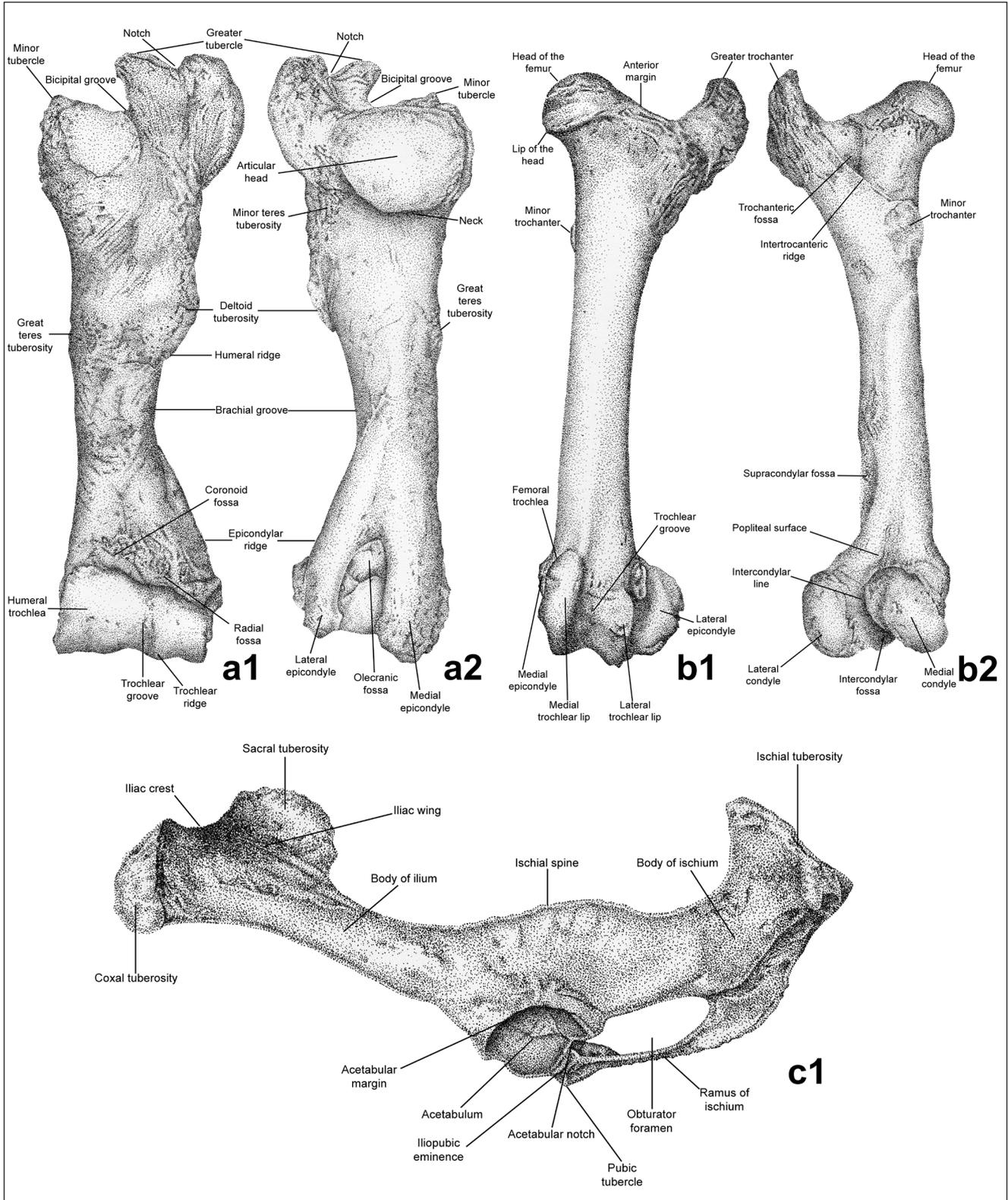


Fig. 2 - Anatomic plate of the *Bison* postcranial indicating the descriptive-diagnostic characters used in the main text: left humerus in anterior (1a) and posterior (1b) view, left femur in anterior (2a) and posterior (2b) view and left coxal bone in lateral view (c1). Artwork by Renata Carmignano.

(1986) and Sorbelli et al. (2023). The measurements are all shown in SD Fig. 2. The comparative material of *Bison* and *Bos* spp. was taken from the litera-

ture. Additional remains of *Bos primigenius* from the Middle Pleistocene of Ponte Molle, housed in the Museo Universitario di Scienze della Terra (MUST),

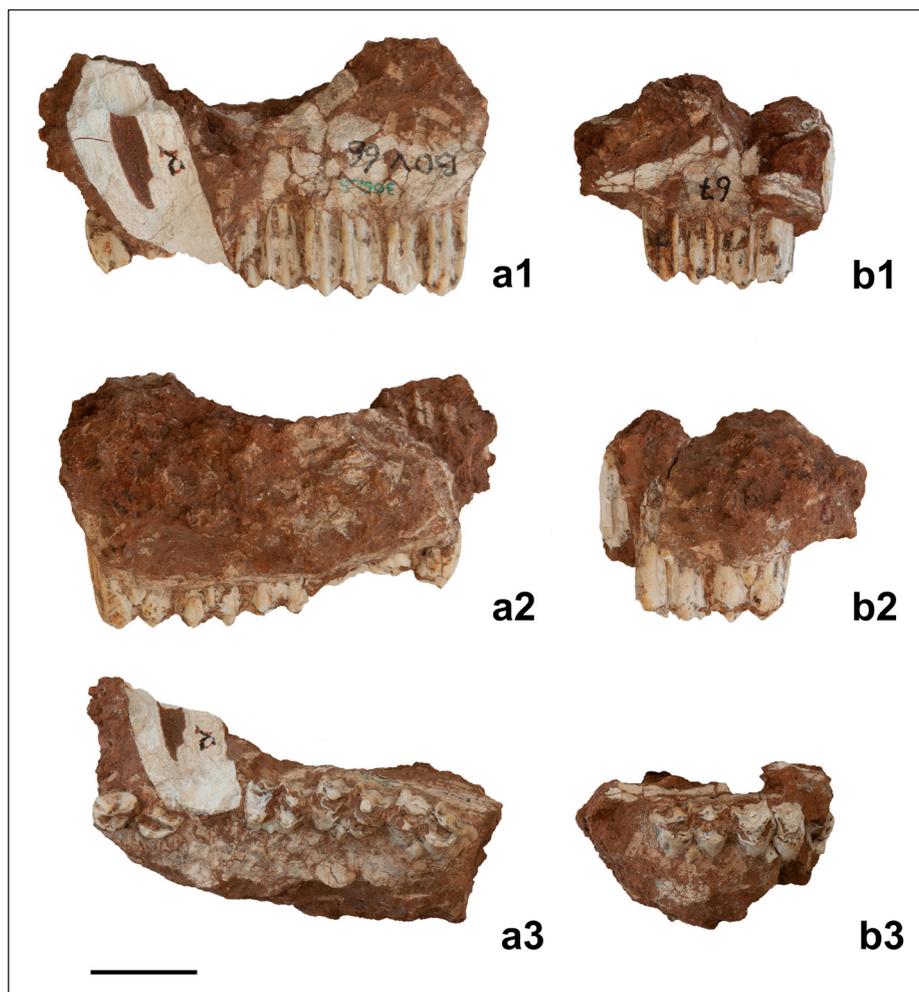


Fig. 3 - Maxillary remains of *Bison* cf. *schoetensacki* from Contrada Monticelli, MSTB - CM 30645, left maxilla (M^1 - M^3) in buccal (a1), lingual (a2) and occlusal (a3) view; MSTB - CM 30646, right maxilla (M^2 - M^3) in buccal (b1), lingual (b2) and occlusal (b3) view. Scale bar 5 cm.

Sapienza Università di Roma, are also included. Bivariate plots of length (L) vs width (W) of upper and lower molars and box-plot of distal end articular width (DEAW) of the humeri and distal end width (DEW) of the femurs, were carried out in order to evaluate the size and proportions between the CM sample and other *Bison* spp. and *Bos* spp. samples. A Log_{10} ratio diagram (Simpson 1941) was performed on the femur to investigate the principal differences between ranges of extinct *Bison* and *Bos* in 5 variables. The extant *Bison bonasus* has been used as standard of comparison (data taken from Reshetov & Sukhanov 1979). All statistical computations were made with PAST v. 4.13 (Hammer et al. 2001). All the aforementioned data and related references, are reported in the Tabs. 2 and 3 in SD.

RESULTS

Morphological description

Eight specimens belong to adult individuals.

The hemimandible MSTB - CM 30643 preserves the M_1 - M_2 and the DP_4 , representing the only early adolescence (A-S in Skinner & Kaisen 1947) specimen. The other two hemimandibles (MSTB - CM 30639 and MSTB - CM 30641) show not completely erupted teeth, indicating a late adolescence age class (S-1 in Skinner & Kaisen 1947). Based on the wear on cusps, no remains can be ascribed to senile individual.

Upper teeth (Fig. 3). Two maxillaries were recovered at CM, MSTB - CM 30645 and MSTB - CM 30646 (Tab. 1).

Fragments of the upper premolars are preserved only on MSTB - CM 30645 and they are in poor condition, fractured and heavily encrusted with sediment. This made it possible to visualize a very limited number of morphological characters. In the molars, the neck has a trapezoidal section and the mesial and distal edges of the crown are rather domed. The styles are protruding and thick, especially the straight mesostyle. In occlusal view the lingual and buccal edges tend to converge forward.

P²- The teeth neck has a trapezoidal section

and on the labial side, the metastyle is protruding and tends to curve slightly forwards.

P³ — In occlusal view, a thick paracone rib and a rather sharp parastyle are visible.

M¹ — The ribs of the paracone and metacone are marked in occlusal view. The central cavities possess several enamel folds, while an enamel islet can be observed in the central part of the tooth. The distal lobe of M¹ of MSTB - CM 30646 shows a “bubaline fold” (sensu Merla 1949). On lingual side, the protocone and hypocone have a strongly convex profile, with the mesial lobe narrower buccolingually than the distal one. The entostyle is short and robust. In labial view, the metacone and paracone show similar width.

M² — In occlusal view, the parastyle and the metastyle are quite robust, while the mesostyle is less developed, but elongated buccally. An enamel islet is present in the central part of the tooth. The enamel folds enclosing the central cavities are quadrangular. On lingual side, the protocone and hypocone have a slightly less convex profile than on M¹, with a similar bucco-lingually width of the two lobes. The entostyle is large and ogival in shape, but does not reach the upper part of teeth in lingual view. In labial view, the paracone rib is also quite elongated buccally.

M³ — The tooth is trapezoidal in shape in occlusal view, with a narrower distal lobe. The protocone and hypocone have a slightly convex profile, with the latter weakly inclined mesially. The entostyle is robust but short, with ogival shape. In labial view, the rib of the paracone is slightly less developed than the metacone one.

Lower teeth (Figs. 4 and 5). Seven hemimandibles were collected at CM, but no lower incisors are preserved (Tab. 2). The conservation conditions are generally good, however, especially in the case of the premolars, the presence of encrusting sediment and other cemented bone fragments do not allow us to visualize different views and morphological characters. The molars generally have a profile that widens towards the neck and narrows towards the apex of the crown. The two main columns of the lower molars are rather close together, thus giving at the teeth a more mesiodistally compact appearance.

P₂ — The tooth is mesiodistally elongated. The protoconid is larger than the hypoconid. Due to the poor state of preservation, it was not possible to evaluate the morphology of the other cusps both in MSTB - CM 30639 and in MSTB - CM 30641.

P₃ — The tooth is mesiodistally elongated, with the protoconid larger than the hypoconid. Parastylid and paraconid are slightly separated and mesially elongated in occlusal view.

P₄ — The tooth is mesiodistally elongated. The parastyle is buccally oriented in occlusal view, and it is lower than the paraconid in lingual view. The latter is separated from the metaconid by a wide and deep sulcus. The metaconid and entoconid are quite close, with the former larger in occlusal view and higher in lingual view than the latter. In labial view, the protoconid and hypoconid are not closely spaced and show similar width.

M₁ — The distal profile of the tooth is rather flattened, while the mesial one more inclined mesiolabially in occlusal view. In lingual view, the parastylid is robust; the metastylid is slightly less marked and it becomes less evident toward the basal portion of the crown. Metaconid and entoconid ribs show a columnar appearance. In labial view, the protoconid and hypoconid are lingually expanded, with a quite wide and deep groove between them.

M₂ — In occlusal view, the inner enamel folds are surrounded by copious cementum. The two halves of the tooth are well separated and of similar proportions. On lingual side, the parastylid is quite robust, and reaches the basal portion of the crown; it is separated from the metaconid by a distinct fold. The metastylid is weak and is separated from the entoconid by an internal fold which is wide and flattened. The entostylid is marked, even if less robust than the parastylid. In labial view, the protoconid and the hypoconid are wide and columnar; they are separated by a deep and rather narrow sulcus filled with enamel. Only in MSTB - CM 30639 is it possible to evaluate the morphology of the ectostylid: it is columnar, of moderate thickness and not very protruding.

M₃ — In occlusal view, the parastylid is robust and separated from the metaconid by a marked U-fold. The metastylid is weak, while the entostylid is robust and quite rounded. The posterior edge of the hypoconulid is quite sharp. In lingual view, many morphological characters are not observable due to the state of preservation or the incomplete eruption of the tooth itself, except in MSTB - CM 30639. In the latter, in fact, the slightly protruding columnar parastylid is visible. In labial view, the protoconid is wide and slightly flattened in profile. The ectostylid is columnar and ends before of the

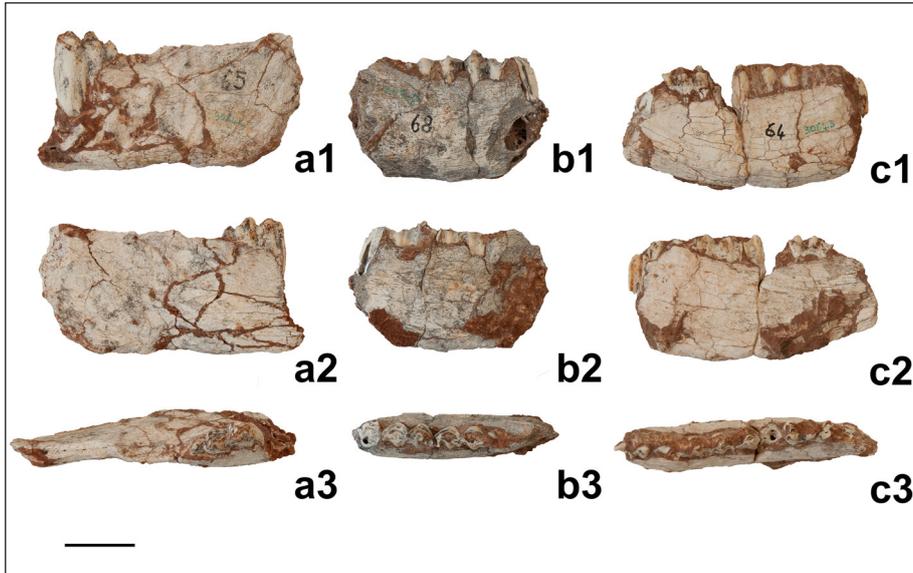


Fig. 4 - Mandibular remains of *Bison* cf. *schoetensacki* from Contrada Monticelli, MSTB - CM 30644, left mandible (M_3) in buccal (a1), lingual (a2) and occlusal (a3) view; MSTB - CM 30647, right mandible (M_2 - M_3) in buccal (b1), lingual (b2) and occlusal (b3) view; MSTB - CM 30643 right mandible (DP_4 - M_3) in buccal (c1), lingual (c2) and occlusal (c3) view. Scale bar 5 cm.



Fig. 5 - Mandibular remains of *Bison* cf. *schoetensacki* from Contrada Monticelli, MSTB - CM 30639 left mandible (P_2 - M_1) in buccal (a1), lingual (a2) and occlusal (a3) view; MSTB - CM 30641 left mandible (P_2 - M_3) in buccal (b1), lingual (b2) and occlusal (b3) view. Scale bar 5 cm.

occlusal surface of the tooth. The sulcus separating the protoconid from the hypoconid is narrow and deep. The hypoconid and hypoconulid are instead separated by a shallow sulcus. The angle formed by hypoconid and hypoconulid is generally right in MSTB - CM 30644 and MSTB - CM 30647, while it is obtuse in MSTB - CM 30639.

Humerus (Fig. 6). Two fragments are present: the first is a complete proximal epiphysis (MSTB - CM 30648), the second a distal trochlea (MSTB - CM 30649). Anteriorly, the minor tubercle is separated from the greater by a rather narrow groove.

The greater tubercle has a large V-shaped notch and posteriorly shows a very marked and thick convexity. It forms an obtuse angle with the bicapital groove (= intertubercular sulcus) and has no noticeable overhang. The floor of the bicapital groove shows a smooth slope from the medial wall of the groove to the base of the lateral tuberosity. The furrow that separates the humeral trochlea from the capitulum is slightly lateral to the midline of the articulation.

Coxal bone (Fig. 7b). A partially preserved right coxal bone was found at CM. In lateral view

Fig. 6 - Postcranial remains of *Bison* cf. *schoetensacki* from Contrada Monticelli, MSTB - CM 30648, left humerus in cranial (a1), medial (a2), lateral (a3), caudal (a4) and proximal (a5) view; MSTB - CM 30649, left humerus in cranial (b1) view. Scale bar 5 cm.

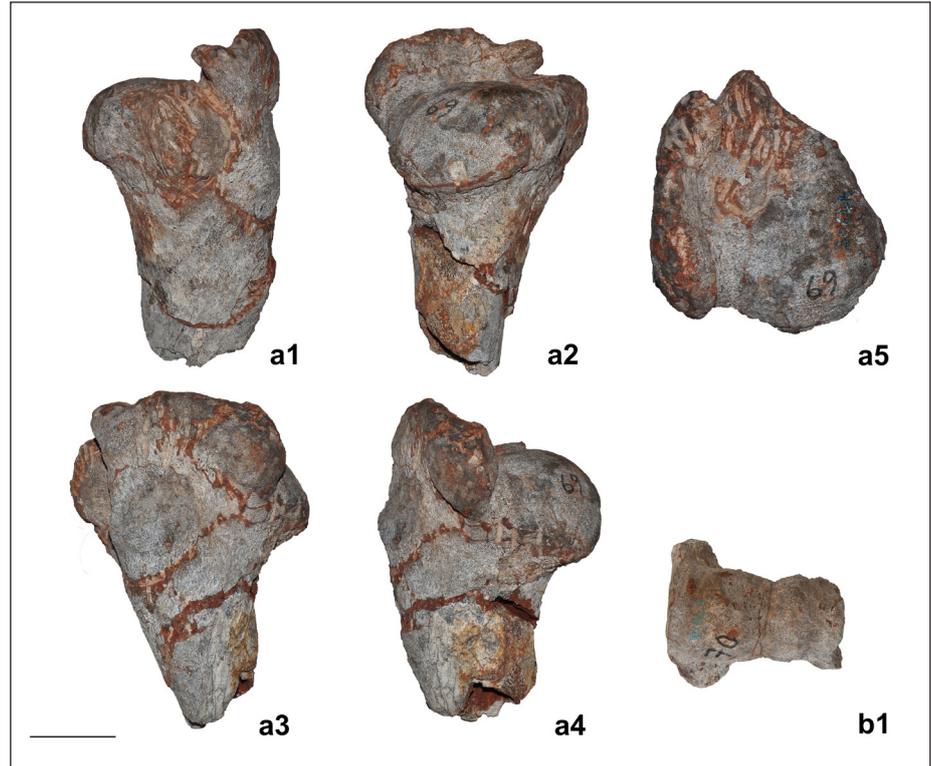
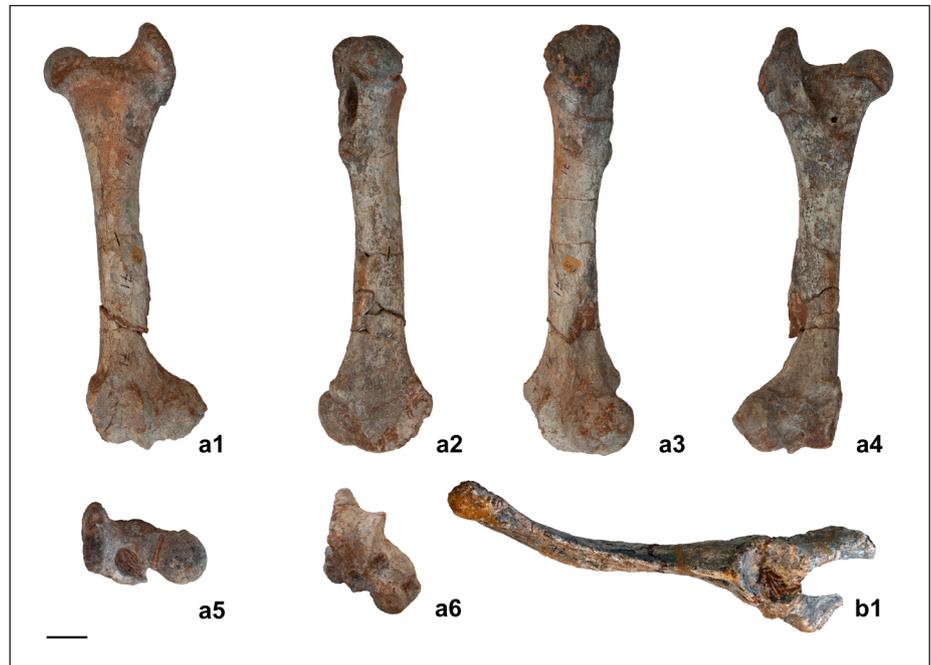


Fig. 7 - Postcranial remains of *Bison* cf. *schoetensacki* from Contrada Monticelli, MSTB - CM 30650, left femur in cranial (a1), medial (a2), lateral (a3), caudal (a4), proximal (a5) and distal (a6) view; MSTB - CM 30651, right coxal in lateral (b1) view. Scale bar 5 cm.



and anteriorly, part of the bone has a large portion of the iliac wing with a thick and rounded marginal contour ending in a robust coxal tuberosity (= iliac spine). The latter shows an ovoid profile when viewed antero-dorsally and more flattened when viewed ventrally. The acetabulum is large and with a sub-spherical cavity. The margin is rather irregular and the acetabular notch is visible in the posterior

part. Below the acetabulum, the iliopubic eminence and part of the pubic bone are visible. These terminate posteriorly with the dorsal pubic tubercle and part of the pelvic symphysis. Posteriorly, a short part of the ischium (ischial spine) surrounds the posterior part of the obturator foramen.

Femur (Fig. 7a1-6). The bone is complete, except for the lack of the medial condyle. In pro-

ximal view, the anterior margin shows a marked re-entrance, furthermore the minor trochanter does not protrude much posteriorly, and the trochanteric fossa is barely visible. In anterior view, the head of the femur, of spheroidal shaped, appears as if projected slightly backwards. Conversely, the greater trochanter is projected slightly forward and has a very protruding crest up to its top. It is also not very extensive laterally and shows a rather smooth cranial margin. The angle between the head of the femur and the greater trochanter is slightly obtuse. The fusion line at the junction of the articular head and greater trochanter forms a smooth curve. The diaphysis is tapered and ends distally in a large epiphysis. In medial view, the medial trochlear lip extends considerably farther in distal direction than does the medial condyle. Posteriorly, a deep and ovoid trochanteric fossa is visible, inclined markedly laterally. Below it, there is a marked tuberosity, corresponding to the minor trochanter. The lateral condyle is large and globular in shape. A slight ligamentous insertion fossa (laterally) and a more marked popliteal fossa (distally) are distinguishable on it. Most of the medial epicondyle and part of the medial trochlear crest are missing. Below the intercondylar line is a deep spheroidal intercondylar fossa. In distal view, between the lateral condyle and the lateral lip of the trochlea, there is an ovoid and rather deep extensor fossa. The axes passing through the trochlear lips are divergent.

MORPHOLOGICAL COMPARISON

Teeth. Following the main morphological characters reported in Sala (1986) and Magnitez (2010), typical bisonine features were found in the upper molars of the CM sample (Fig. 3). For example, a trapezoidal section of the neck, somewhat rounded bases of the mesial and distal edges, a straight mesostyle, and converging buccal and lingual edges were observed in both maxillary specimens. Furthermore, on both finds and in three cases the presence of an islet of enamel was found between protocone and hypocone (Figs. 3a3 and b3). This character distinguishes *B. (Eobison) spp.*, *B. menneri* and *B. schoetensacki* from *B. priscus* and *Bos primigenius*, in which it is rare (Prat 1968; Sala 1986; Sorbelli et al. 2021). This character is also consistent with what has been observed in *B. schoetensacki* from Isernia La Pineta and other European sites (Sala 1986), such as the

Spanish site of Vallparadís Estació, where it is present in almost all teeth at a medium-advanced stage of wear. Above the neck, a swelling at the begins of enamel occurs like in *Bison* and contrary to what happens in *Bos*, which has a more columnar appearance (Sala 1986). The amount of cement present is considerable, especially between the folds on the lingual side; this trait may have a diagnostic value, as it is quite scarce or absent in *Leptobos* and more commonly found in *Bison* (Sorbelli et al. 2023). The presence of rather thick stylid as well as the less developed entostyle are closer to *Bison* than to *Bos* (Sala 1986). In lower teeth (Figs. 4 and 5), the P₂s of CM show a more delicate and thin appearance than that more typically found in *Bos* (Magnitez 2010) (Figs. 5a1 and 5b1). The compact appearance of the molars mesiodistally is closer to *Bison* than to *Bos* (Sala 1986) the molars ectostylids are short and overall have an inverted V-shaped profile, both characteristics associated with *Bison* (Sala 1986; Magnitez 2010). As far as M₃ is concerned, the labial reentrance between the hypoconid and hypoconulid (Fig. 4a3) is generally less angular than that typical in *Bison*, appearing almost as something between *Bison* and *Bos*.

Humerus. The humerus from CM (Fig. 6) has the typical notch along the upper edge of the greater tubercle which is present in *Bison* and absent in *Bos* (Sala 1986; Martin 1987) and there is no trace of intermediate tubercle, as in *Bison* (Martin 1987). In *Bos* the medial point of the greater tubercle (= lateral tuberosity in Olsen 1960) overhangs the bicipital groove, while in *Bison* this same projection is directed to form an obtuse angle of the bicipital groove and has no noticeable overhang (Olsen 1960). Furthermore, the floor of the bicipital groove, in *Bison*, slopes even from the medial wall of the groove to the base of the greater tubercle, while in *Bos* the bases of the minor tubercle (= medial tuberosity) and greater tubercle are separated by a pronounced swelling (Olsen 1960). In MSTB – CM 30648 (Fig. 6a1-5), the floor of the bicipital groove does not show swelling and slopes in a similar way to what is observed in *Bison*. The trochlea (Fig. 6b1) shows a rather flattened ridge and a shallow trochlear groove, as observed in *Bison* by Martin (1987); this feature differs significantly in *Bos*, that has a higher trochlear ridge and a deeper groove.

Coxal bone. The marginal outline of the ilium near the coxal tuberosity ends in a highly thick and

rounded shape: this is a typical condition in *Bison* and differently from the very roughened margin present in *Bos* (Olsen 1960; McCuaig Balkwill & Cumbaa 1992). The same coxal tuberosity, seen anterodorsally, has an ovoid profile, while ventrally it has a flattened profile (Fig. 7b1). Both these features are typical of the pelvis in *Bison*.

Femur. Complete femurs of *Bos* and *Bison* are exceptionally rare in the Eurasian fossil record; thus, the CM specimen is quite important in the understanding of the morphology and proportions of these bones in large bovines. In proximal view (Fig. 7a5), the anterior margin is recessed and not straight; furthermore, the minor trochanter is little protruding posteriorly and the trochanteric fossa is less visible. Both of these morphologies are associated with *Bison* rather than *Bos* (McCuaig Balkwill & Cumbaa 1992). In anterior view (Fig. 7a1), a noticeable ridge between the head of the femur and the trochanter minor is not present in CM sample, as typically in *Bison*. On the contrary, a defined raised area separating the trochanteric fossa from the neck of the femur is typical of *Bos* (Olsen 1960; McCuaig Balkwill & Cumbaa 1992). The head of the femur does not form an obvious lip, however it appears very distinct from the neck. In *Bison* it has a slight tendency to form a lip at its junction with the neck rather than a blending of these two areas, as observed for *Bos* (Olsen 1960). The proximal epiphysis shows a slightly obtuse angle between the articular head and the greater trochanter. Several other features of the proximal end mirror the typical morphologies found in *Bison* rather than *Bos* (see McCuaig Balkwill & Cumbaa 1992). For example, in anterior view the fusion line at the junction of the articular head and greater trochanter is similar to the typical *Bison* morphology, in which it forms a smooth curve; conversely, in *Bos* this line curves approximately at right angles. Similarly, laterally (Fig. 7a3), the greater trochanter shows a smoother cranial margin as in *Bison*, versus the more angular one present in *Bos*. Always laterally, the connecting part between the articular head and the minor trochanter is elongated and has an almost vertical trend, like in *Bison*. Again, as typically occurs in *Bison*, the minor trochanter is not very protruding and appears to have a reduced antero-posterior depth as opposed to what can be observed in *Bos*. The shape of the distal epiphysis (Fig. 7a6) is the most remarkable peculiarity of this bone. Above all for the trochlea medially displaced

and the significative difference in the development of the epicondyles. The axes passing through the slightly divergent trochlear lips are associated with the condition observed in *Bison*; conversely, *Bos* tends to have an approximately right angle and axes that run parallel (Martin 1987).

BIOMETRIC COMPARISON

The lengths (L) and widths (W) of the upper and lower molars of several extinct species of Bovinae were compared (Fig. 8). Although a strong overlap among the different species is evident, some trends have emerged. *Bison deginlii* Masini, Palombo & Rozzi, 2013 is the species that shows the smallest dimensions in the lower molars and, on the other hand, a wide range of variability in the length of the upper molars. *Bison menneri* generally occupies the middle part of the graphs, showing slightly larger sizes in M₁ and M₂ (Figs. 8d and 8e). The molars of *Bison schoetensacki* always occupy the central parts of the plots, displaying a huge range of variability along the length axis, especially for the upper molars (Fig. 8d-f). *Bison priscus* is the species that generally has the largest molars overall. Measurements of molars in *Bos primigenius* cover the central parts of the graphs, featuring wider teeth when compared with *B. schoetensacki*. The CM sample often appears similar to *B. schoetensacki*, even if in several cases it tends to occupy peripheral positions in the range of variability of this species (es: Fig. 8a-c).

The biometric comparison of the distal end articular width (DEAW) of the humerus (SD Fig. 3) highlighted an interesting dimensional pattern. The humeri show an increasing size passing from *Leptobos* spp. to *B. priscus*, whereas there is an inverse trend in the extant species *Bison bonasus*, which stands at lower values, similar to the ones shown by *Leptobos* spp. The CM humerus falls within the variability of the extinct *Bison* species, larger than both *Leptobos* spp. and *B. bonasus*. In spite of that, the Apulian specimens falls slightly below the average of *B. menneri* and rather close to the larger forms of *Eobison* spp. The size of the trochlea of the humerus from CM is rather small if compared to that of *B. schoetensacki* from Le Vallonnet (France ca. 1.2-1.1 Ma; Moullé 1992), Vallparadís Estació (Sorbelli et al. 2021) and Isernia La Pineta (Sala 1986), but is closer to that of Mauer Pleistocene woodland bison (Germany, ca. 0.4 Ma; Sala 1986).

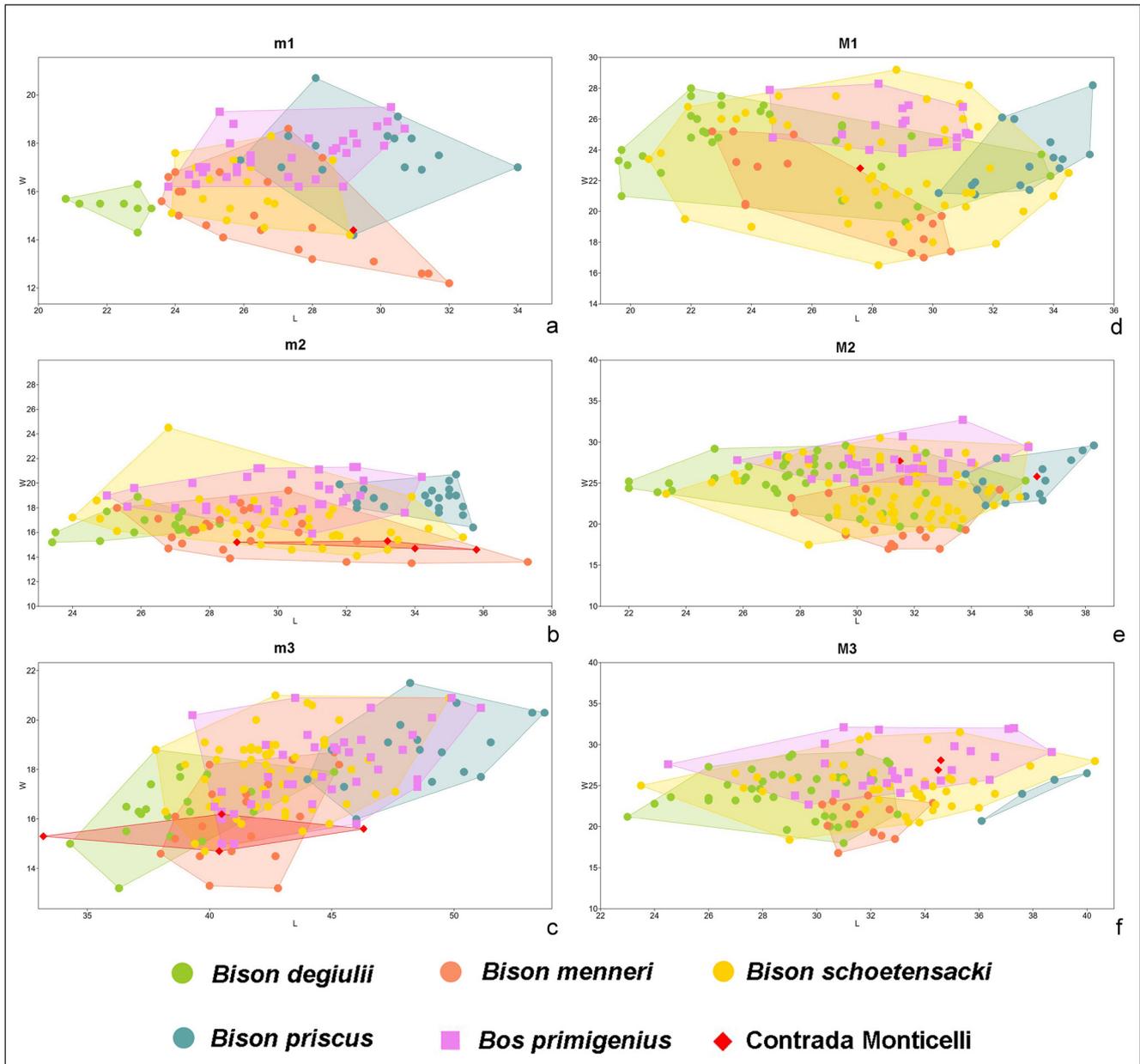


Fig. 8 - Bivariate plot of length (L) and width (W) of lower (a, b and c) and upper (d, e, and f) molars. Data are taken from Cerilli (1989); Masini (1989); Moullé (1992); Brugal (1995); van Asperen & Kahlke (2017); Kostopoulos et al. (2018); Sorbelli et al. (2021); Sorbelli et al. (2023) and this work. Other data are explained in Tab. 2 in Supplementary Data.

The boxplot of the distal end width (DEW) of the femur (SD Fig. 4) shows an overall increase in size from *Leptobos etruscus* to *Bison priscus*. The extant *B. bonasus* stands at values like those of *B. priscus*. The only specimen of *B. primigenius* possesses the widest distal end. The CM femur appears very close to the average of *B. bonasus* and *B. priscus* and slightly below the only available specimen of *B. schoetensacki*. Conversely, the studied specimen it is significantly greater than *Leptobos etruscus* (Falconer, 1868), *Bison degiulii* and *Bison menneri*.

The comparison between the measurements of the femurs of the different Bovine species carried out using Log_{10} ratio diagram (Fig. 9) has revealed that the CM bison has a relatively large size in all the considered variable. The studied femur is larger than those referred to the extinct *Leptobos etruscus*, *Bison degiulii*, *Bison menneri* and the *Bison bonasus*. The CM specimen fits well within the group of large forms including *Bison priscus*, *Bison schoetensacki* and *Bos primigenius*. The two specimens of *B. schoetensacki* used in this comparison are particularly large, even

more massive than the analyzed *B. priscus*. The CM specimen is smaller than the two *B. schoetensacki* in most of the measures, better fitting with the steppe bison *B. priscus*. However the scarcity of the sample referred to *B. schoetensacki* (2 specimens) does not allow to infer properly on the morphometric variability of this species.

DISCUSSION

Morphologic and biometric remarks

The presence of a large bovid (*Bos* vel *Bison*) at CM was reported by Mazza & Varola (1999), but never properly studied. The morphological analysis carried out here on the dental and postcranial remains of CM shows the presence of features typical of the genus *Bison*, including: a trapezoidal section of the tooth neck, somewhat rounded bases of the mesial and distal edges of teeth, straight mesostyle, converging buccal and lingual edges of the upper molars, and the presence of the typical notch along the upper edge of the greater tubercle in the humerus. Although some identified characters in the CM sample are shared also with other large *Bison* species (e.g., *B. priscus*), most of the features, such as teeth morphology, are very similar to the Early-Middle Pleistocene *Bison schoetensacki*. In particular the presence of an islet of enamel between protocone and hypocone in the maxillary teeth distinguishes *B. schoetensacki* from *B. priscus*. In addition, the CM sample often appears similar to *B. schoetensacki*, even if in several cases it tends to occupy peripheral positions in the range of variability of this species. Considering the scanty nature of the studied sample and the lack of the most diagnostic elements (e.g., horncores, skulls and metapodials) the remains from CM are prudently ascribed to *Bison* cf. *schoetensacki*.

The biometric comparison carried out on the teeth shows how the CM bison generally falls in the variation range of *B. schoetensacki* showing a smaller size compared to the quite massive *B. priscus* teeth. Nevertheless, the degree of overlap among *Bison* species is quite high in many cases suggesting a cautious approach to the interpretation of the data (Fig. 8). The biometric analyses performed on the postcranial bones revealed that the overall measurements of the CM specimens do not differ significantly from large sized *Bison* of Epivillafranchian-Galerian -i.e. *B. schoetensacki* and *B. priscus*- (SD

Figs. 3 and 4). The Log_{10} ratio diagram of the femur (Fig. 9) highlights a strong affinity between CM sample, and the aforementioned group. However, it is necessary to consider the influence of the sexual dimorphism that may concern the long bones of Bovinae taxa, where the males are generally larger and more robust than females (Schertz 1936a, b; Brugal 1985; Sher 1997; Drees 2005). This could affect significantly the interpretation of the data especially when dealing with small samples such as in this case. The general size trend toward gigantism is recognized in our biometric comparison, both on the teeth and on the postcranial elements. In fact, the Early Pleistocene forms are reduced in size when compared with the Middle and Late Pleistocene taxa. The evolutionary tendency to increase in body size within the same lineages or even taxon through time, known as Cope's "rule" (1887), was already detected in the genus *Bison* (see Maniakas & Kostopoulos 2017).

The herbivore faunal assemblage and paleoenvironmental implications

In the CM site, in addition to *Bison* cf. *schoetensacki* identified in this work, other herbivores have been recognized, such as *Palaeoloxodon antiquus*, *Stephanorhinus hundsheimensis*, *Dama* cf. *roberti*, and *Equus* sp. . The composition of the faunal assemblage may offer important information about past environments, especially the herbivores that are intimately linked to vegetation. Based on the dietary interface as a pathway, combined with some morphological features, the mammal assemblage may provide subtle insights into the reconstruction of Quaternary terrestrial ecosystems (Kahlke & Kaiser 2011).

Palaeoloxodon antiquus appears to be strongly linked to temperate, wooded or mixed vegetational conditions (Stuart 1982), but some records suggest an ability to adapt to semi-open conditions (Lister et al. 1990). Lister (2004) conceived this species as a woodland-adapted animal with a mixed browse and graze diet. *Stephanorhinus hundsheimensis* was a long-legged rhinoceros with cursorial limb-proportions and a head posture that presumably allowed the animal to feed both as a grazer and browser on vegetation of intermediate height. In fact, *S. hundsheimensis* was undoubtedly the most ecologically tolerant rhinoceros of the Pliocene-Pleistocene Palaeoarctic (Kahlke & Kaiser 2011). Recently, Zanazzi et al.

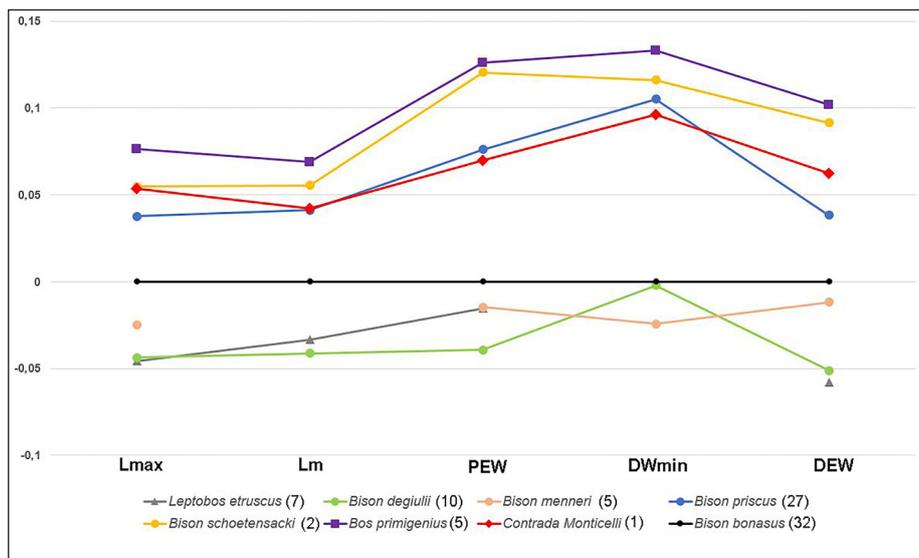


Fig. 9 - Log₁₀ ratio diagram of femur in several species of Bovinae. Data are taken from Duvernois (1990), for *Leptobos etruscus*; Masini (1989) and Sorbelli et al. (2023) for *Bison degiulii*; Sher (1997) for *Bison menneri*; Martin (1987) for *Bison schoetensacki*, *Bison priscus* and *Bos primigenius*; Sala (1986), Guérin & Valli (2000), Prat et al. (2003), Vasiliev (2008), Castaños et al. (2012) for *Bison priscus*; Reshetov & Sukhanov (1979) for the standard *Bison bonasus*. In brackets the number of specimens for each species. Other data are explained in Tab. 3 in Supplementary Data.

(2022) analyzed carbon and oxygen stable isotopes of the tooth enamel of *S. bundsheimensis* from Isernia La Pineta (MIS 15, southern Italy) with the aim of reconstructing the paleoclimate and paleoenvironment of that area very close to CM both geographically and chronologically. The results indicated that the ecosystems were dominated by woodlands and/or grasslands, with the possible sparse presence of closed canopy forests. Added to this mosaic of ecosystems is a seasonally uniform climate and average annual temperatures similar to those today. *Dama cf. roberti* is probably another generalist herbivore, capable of adapting to both wooded habitats and steppe. In support of this, the modern *Dama dama*, a close relative species still living, has a generalist diet, with a large adaptability to thrive in different ecosystems and with a vast spectrum of food preferences (Esattore et al. 2022; Mecozzi et al. 2023). Based on mesowear values, Pushkina et al. (2020) determined that Cervidae (*Cervus*, *Dama* and *Megaloceros*) and Rhinocerotidae (referring to *Stephanorhinus*, with the exception of *Coelodonta*) had a mostly browse-dominated diets and that these ungulates inhabited mostly dense forests to woodlands and shrublands. The Middle Pleistocene fallow deer of Casal Selce (MIS 15, central Italy) attributed to *Dama* sp. (Strani et al. 2021) is the only species in the site displaying mesowear patterns consistent with a browsing behavior. Casal Selce is close to CM both geographically and chronologically, furthermore it presents a similar composition of animals capable of exploiting different types of vegetal resources with browsers, greezers and mixed feeders. The

presence of equids at the CM site is evidenced by the presence of the distal portion of a tibia indicating the presence of open environments.

Maniakas & Kostopoulos (2017) suggested the adoption of a dietary flexibility by *B. schoetensacki* populations from the steppe-like open biome of Süssenborn to the grassland with sparse forest of Isernia La Pineta (Arobba et al. 2004). Van Asperen & Kahlke (2017) suggested that the general trend within the bison group appears to be in the direction of greater adaptation to open landscapes and it supports the conclusion that an increase in forest cover poses a disadvantage for bison nutrition. Sorbelli et al. (2021) suggested that the increase of limbs stoutness corresponded to more arid conditions, and slenderness to more humid ones, tracing this trend in several *B. schoetensacki* samples. Flerov (1979) also stated that the slenderer and taller forms of *Bison* are better adapted to closed and forested environments as opposed to the stouter ones, which are more suited to open and arid conditions. The slenderer forms of *Bison* as the long-legged *B. menneri* from Untermassfeld or the samples of *B. schoetensacki* from Le Vallonnet and Mauer are found in more humid, heterogeneous habitats (i.e., mosaic of forested and open patches), while the samples of *B. schoetensacki* from more arid sites such as Süssenborn, Durfort and Vallparadís Estació exhibit stouter proportions (Sorbelli et al. 2023). The CM bison shows elongated, but rather slender limbs. For example, the femur is very similar in length to the Mauer and Mosbach specimens, but overall it is on average slimmer (Fig. 9). Therefore, the exist-

tence of an herbivore taxon with such flexible feeding habits in the CM site could be coherent with the presence of a relatively heterogeneous forest-grassland ecotone, suitable for grazing or browsing diet.

The *Bison* record in Europe: an overview

The presence of *Bison schoetensacki* in Europe shows a scattered distribution which can be related either to an asynchronous dispersal of the species and/or to taphonomic bias. Most of the record referable to this species is concentrated in the western Mediterranean area including the Italian peninsula, southern France up to North-East Iberian Peninsula (Sorbelli et al. 2021). The presence of this bison in central Germany and southern Britain is included in the same longitudinal bands as the previous sites, albeit at significantly higher latitudes and younger chronologies. In eastern Europe *Bison schoetensacki* is considered a common element of the so-called Tiraspolian faunal complex (ca. 0.9–0.4 ma) given the abundant remains from Kolkotova Balka (Moldova) although some authors contested the taxonomical attribution (e.g., *B. aff. priscus* according to Sher 1997).

In the southern Balkans, the early bison (i.e., subgenus *Eobison*) arrived between 1.7 and 1.5 Ma and most likely coexisted with the last *Leptobos* for a short period, as suggested by the Tsiotra Vryssi (Greece) and Trlica (Montenegro) sites (Kostopoulos et al. 2018). However, there is no adequate record of lower Middle Pleistocene bison in that region, so the history of the taxon in the area during the Epivillafranchian is much less known. The first reliable record of bison in the southern Balkans occurred in the upper Middle Pleistocene faunas of Petralona cave (North Greece) (Tsoukala 1989) and in Megalopolis Basin (Southern Greece; Melentis, 1966) with the large “priscoid” forms that were rapidly expanding across Europe at that time (Kostopoulos et al. 2018). Kostopoulos et al. (2018) refer the bison from Mygdonia Basin (Greece, 1.8–1.0 Ma) to the species of primitive bison *B. (Eobison) cf. deginlii* and suggest that this taxon spread the Italian peninsula and in the Balkans almost simultaneously. The youngest of the fossiliferous sites of Mygdonia basin is that of Apollonia 1, (ca. 1.2 Ma) and presents a faunal context rather similar to that of Pirro Nord where the same species was found (Masini et al. 2013). *Bison deginlii* is already present in Italian territory as testified by the rich record from

Pietrafitta (1.5 Ma; Sorbelli et al. 2023) and its presence seems to extend up to 0.8 Ma, as suggested by the Ellera di Corciano sites (Cherin et al. 2012) and Cava Redicicoli (Marra et al. 2014) although these latter two taxonomical attributions have to be confirmed. The chronological reassessment of Pirro Nord, constrained between 1.0 Ma and 0.8 Ma (Duval et al. 2024), would become one of youngest sites, altogether with Apollonia 1, that hosted the primitive subgenus *Eobison*. A possible co-presence of two bison species seems to have occurred in Untermassfeld (central Germany, ca. 1.0 Ma). This location is known due to the presence of *Bison menneri*, considered one of the first “true” *Bison* (Sher 1997) populating Europe. Recently, Bukhsianidze (2020) refers *B. menneri* to the yak, subgenus *Bison (Poepbhagus)*, and points out to the presence at the site of a juvenile skull and a single metacarpal which are referable to an undefined second species of bison. During the Middle Pleistocene, remains of *B. cf. schoetensacki* are present in Mosbach (central-western Germany) characterized by rather “priscoid” proportions (Sala 1986; Sorbelli et al. 2021). According to many authors the co-occurrence of *B. schoetensacki* and *B. priscus* in the site cannot be excluded (Sher 1997; Sorbelli et al. 2021, among others), but the presence of two levels of different ages at the site (Mosbach 1 and Mosbach 2) must be considered and the historical collections need a revision to define the taxonomy and the level provenance of the Mosbach bison. By the early Middle Pleistocene, large bison were already populating the British island as testified by the southern Great Britain sites as the Cromer Forest-bed Formation, Boxgrove and Westbury (ca. 0.7–0.4 Ma; Breda et al. 2010). The material from Cromer Forest-bed Formation localities is referred to *B. schoetensacki*, whereas the small sample from Boxgrove is more questionable and assigned to *Bison* sp.; finally the Westbury bison, due to its particular robustness, was referred to *B. cf. priscus* (Breda et al. 2010; Sorbelli et al. 2021). This evidence underlines that, during the late Early Pleistocene (ca. 1.1–0.8 Ma), *B. schoetensacki* most likely coexisted in Europe with at least two other bison species, such as *B. menneri* and *B. deginlii*. During the early Middle Pleistocene (ca. 0.7–0.6 Ma), *B. schoetensacki* appears to have been the only dominant bison species on the European continent, before being progressively replaced by *B. priscus* around 0.5–0.4 Ma (Sorbelli et al. 2021 and reference there-

in). This apparent reduction in bison diversity can also be linked to the arrival of *Bos primigenius* in Europe at ca. 0.5–0.4 Ma. In any case, *B. schoetensacki* seems to have demonstrated a certain adaptive capacity that allowed it to successfully compete with at least one other bison species during the late Early Pleistocene. The presence of a large form of *Bison*, referable to *B. cf. schoetensacki*, in Contrada Monticelli is relevant for the Pleistocene geographical distribution of this Bovinae, representing the southernmost occurrence of this taxon in Europe. This record in the Apulia region would be added to the known reports of this taxon in the early Middle Pleistocene Italian sites of Cesi (MIS 17; Sorbelli et al. 2023), Val di Chiana (Early-Middle Pleistocene; Azzaroli 1984), Notarchirico (MIS 17–16; Cassoli et al. 1999; Moncel et al. 2023) and Isernia La Pineta (MIS 15; Sala 1986). To these records, the dubious reports from Silvia (?MIS 21–19; Bon et al. 1992) and Cava Redicicoli (MIS 20; Sorbelli et al. 2023) are added. The presence of *B. schoetensacki* in continental Europe is already well documented from 1.2–1.0 Ma as demonstrated by German, French and Spanish sites discussed previously. This suggests that the arrival of this species in the Italian peninsula (and perhaps also in the Balkans) did not happen until the early Middle Pleistocene and, vice versa, the late forms of *Eobison* (e.g. *B. degiulii*) remained longer, possibly coexisting with the larger relative for a short period of time. All of this might be linked to the peripheral position and the particular physiography of the Italian territory which on the one hand may have delayed the spread of the “true” *Bison* and on the other allowed the last *Eobison* to persist. The reappraisal of historical collections and new discoveries of Epivillafranchian bison remains from the Italian Peninsula are of the southernmost importance in order to detangle this interesting mystery.

CONCLUSIONS

The sample of bovids studied here for the first time from the Contrada Monticelli site, revealed the presence of a large bison, here assigned to *B. (Bison) cf. schoetensacki*. The study of the dental and post-cranial remains also revealed the presence of individuals with “priscoid” characteristics, as evidenced, for example, by the complete femur. Despite this, the majority of the sample show mor-

phologies and sizes, which are better fitting with the Epivillafranchian–Galerian form *B. schoetensacki*. The CM faunal assemblage, now enriched with a further element, once again shows its close correlation with the Isernia Faunal Unit. In particular, the herbivorous fauna is composed of species adapted to a certain dietary flexibility, which suggests the presence of a relatively heterogeneous environment, with alternation of open grazing areas and areas with denser woody-forest type vegetation. The presence of *B. cf. schoetensacki* in the Apulian peninsula, constitutes further confirmation that this species also occupied the southern part of the Italian peninsula and it represents the southernmost finding of this species in Europe. Dental and postcranial variability between different Pleistocene bison species requires further study, as the co-occurrences between different species and the timing of their succession need to be further clarified.

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