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Mammoths, Deer, and a Dog: Fossil and (Sub) Recent Allochthonous Remains from the Northeastern Croatia (Podravina Region), with the First Radiocarbon Dating of the Croatian Woolly Mammoths (*Mammuthus primigenius*)

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Abstract: Eight anatomically and taxonomically different finds are presented in this paper, and they belong to four taxa: woolly mammoth (*Mammuthus primigenius*), giant deer (*Megaloceros giganteus*), red deer (*Cervus elaphus*), and dog (*Canis familiaris*). All specimens represent allochthonous Late Pleistocene and Holocene animal remains, and all were dredged during the gravel exploitation at the Sekuline site near Molve (Podravina region, SW Pannonian basin, NE Croatia). Mammoth remains (bone and tusk fragments) were radiocarbon dated, and these are the first absolute dates on mammoths in Croatia. One upper last left deciduous premolar (dP4 sin.) also belongs to the same species. Ascribed to a dog is one well-preserved skull with a peculiar abscess scar on the maxillary bone as the result of an inflammatory process on the carnassial (P4) premolar. The Late Pleistocene cervid remains are giant deer, while the other cervid finds were determined to be red deer of the Holocene age. Morphometrical and taphonomical data are presented for each specimen. Such fossil and recent bone/tooth aggregates are characteristic of fluvial deposits and selective collecting. Although lacking stratigraphic provenance, these finds help to fulfil the gaps in palaeoenvironmental, palaeoecological, and palaeoclimate reconstructions of Podravina and its neighbouring areas.

Keywords: allochthonous finds; woolly mammoth dating; cervids; dog; morphometrics; Late Pleistocene; Holocene; Drava river; Croatia

1. Introduction

Gravel pits in Sekuline (46°7′ N, 17°4′ E, 120 m a.s.l.) are situated near the town of Molve (NE Croatia; Figure 1) in Podravina region, which is located in the southwestern part of the Pannonian basin. This central-eastern European basin is bounded by the Carpathian, Alpine, Rhodope and Dinaric mountain belts [1]. Alluvial depressions of the Danube, Tisa, Drava, and Sava rivers are indicative of the Pannonian basin. Furthermore, these alluvia are characterized by different fluvial deposits such as clays, sands, gravels and loess. Sekuline is one of the most recently discovered sites of allochthonous fossil and subrecent to recent mammal skeletal remains in Croatia. The gravel exploitation at the Sekuline area began approximately 20 years ago, when large quantities of gravels and sands were extracted from the Drava alluvium, forming approximately 30 lakes in the surroundings.

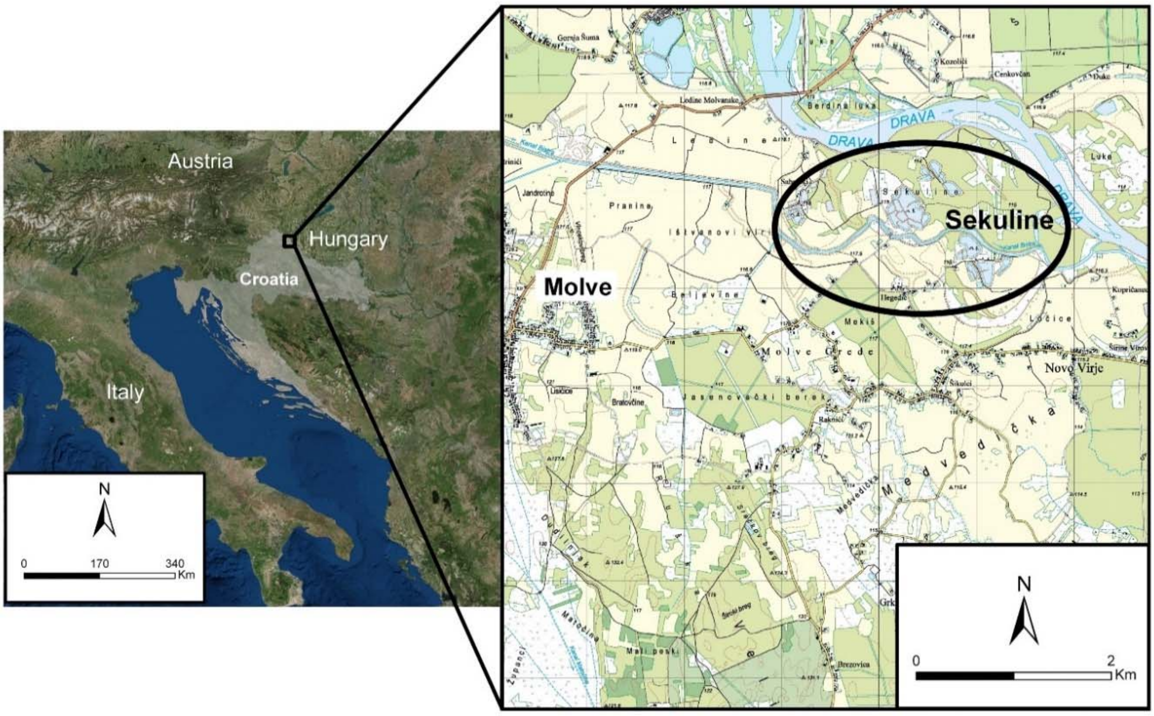

Figure 1. Geographic position of the Sekuline site near Molve (Podravina region, NE Croatia), marked with the ellipse. Map modified after sources: Esri (Redlands, CA, USA), and Geoportal (Zagreb, Croatia, geoportal.dgu.hr).

In 2010, during the gravel exploitation in one of the Sekuline lakes, a few animal remains were dredged. Later, one of the authors (VB) brought these finds to the Institute for Quaternary Paleontology and Geology of the Croatian Academy of Sciences and Arts in Zagreb for determination and paleontological analyses.

Such finds are relatively common in Croatian Late Pleistocene/Holocene fluvial sediments. Numerous skeletal remains of different mammal species have been discovered, mostly during the exploitation of the rivers' gravels and sands [2–5], but sometimes as isolated finds on the riverbanks. Here, we present an allochthonous assemblage representing typical Late Pleistocene (woolly mammoth and giant deer) to Holocene (red deer and dog) remains. Woolly mammoth finds are known from about 100 localities in Croatia [4] (Mauch Lenardić, unpublished data), but on presented remains from Sekuline the first radiocarbon datings on mammoths' specimens were done so far. Unlike mammoths, the finds of giant deer, red deer and dog are not so common. Although the specimens are of unknown stratigraphic position, they are useful for palaeobiogeographical, palaeoclimatological, and palaeoenvironmental reconstructions for this region. Moreover, they also reveal some interesting osteological and pathological scientific data, here presented on a dog skull. Taphonomical analyses and comparisons to the contemporaneous remains from the neighbouring countries have been also presented.

2. Material and Methods

The presented material originates from one of the Sekuline lakes/gravel pits. The bones, antlers, and teeth belong to the following species: *Mammuthus primigenius* (the finds used for the radiocarbon dating were not available for palaeontological analyses), *Megaloceros giganteus*, *Cervus elaphus*, and *Canis familiaris*.

The material was determined and analysed at the Institute for Quaternary Paleontology and Geology of the Croatian Academy of Sciences and Arts in Zagreb, using comparative material from the Institute's collections, as well as the data from the literature.

The fossil/subfossil/recent remains were prepared with polyvinyl butyral (PVB) solution, in which the bones/teeth and antlers were submerged for 1 week, after which they were dried at room temperature.

The specimens were measured by using a digital calliper with an accuracy of 0.05 mm. The measurements (Figure 2) reported in the text and Tables 1–3 are in millimeters (mm) and were taken following von den Driesch ([6], Figure 14a–d and Figure 15a–c) and Zinoviev ([7], Figure 3).

For the metrical comparisons to other Croatian canid specimens (see Table 1), the literature data for four *Canis familiaris* skulls from the Early Bronze Age (Vučedol site, Eastern Slavonia region) [8], one recent golden jackal (*C. aureus*; Slavonia region; borrowed for the analysis), and one recent female grey wolf (*C. lupus*; Lika region; leg. I. Igalffy, stored at: Institute for Quaternary Paleontology and Geology; no inventory number) were used.

Measurements for other anatomical elements (skull with antler, maxilla with teeth, deciduous premolar, atlas, metacarpus, and tibia) are reported in the subsection that describes the particular species. For the isolated antler fragment, no metric values are provided.

The radiocarbon datings were performed in 2012 at the Ruđer Bošković Institute in Zagreb (Croatia), at the Division of Experimental Physics, Laboratory for Low-level Radioactivities. Collagen was extracted from the bone samples, burned to CO_2, and then transferred to benzene. The ^{14}C activity of benzene was measured by liquid scintillation counter (LSC; Quantulus 1220) [9]. The results are expressed in conventional ^{14}C age (BP) and median value.

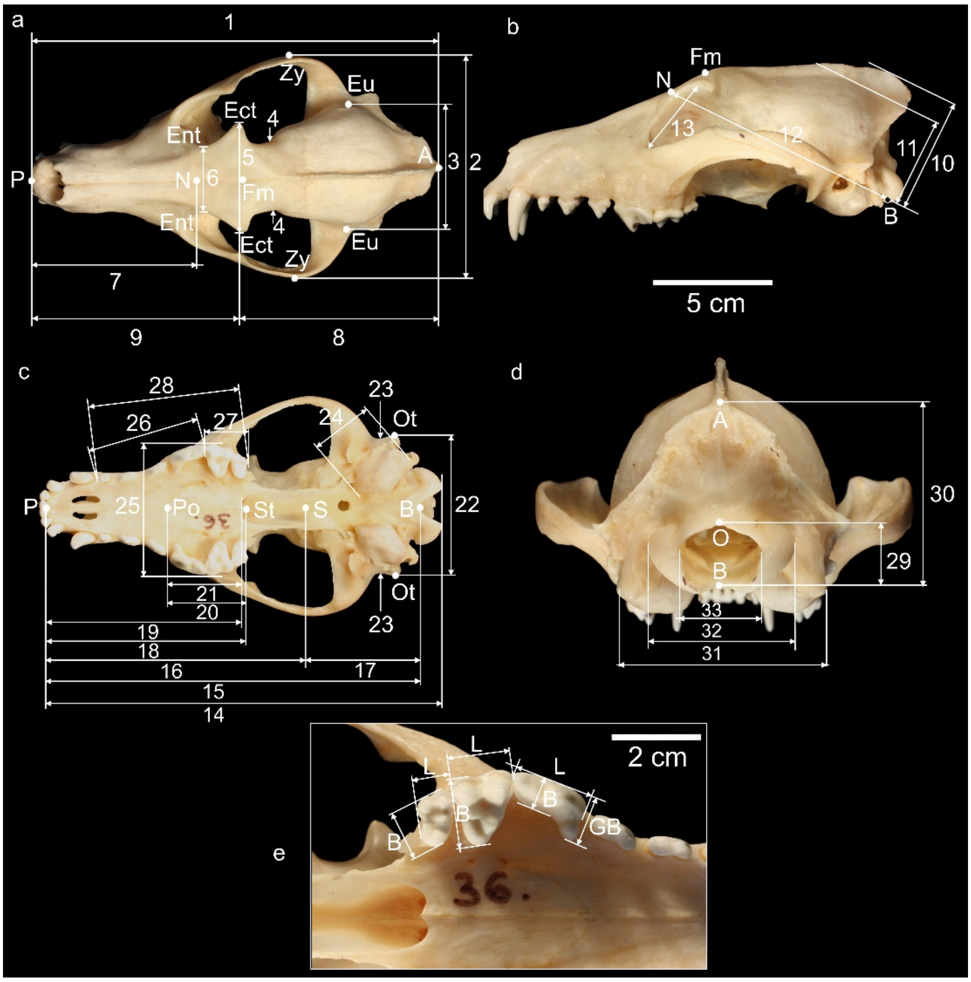

Figure 2. Golden jackal (*Canis aureus*) skull with measured craniometric parameters on the specimens presented in this paper (partly after [6,7]): (**a**)—dorsal, (**b**)—lateral (left), (**c**)—basal, (**d**)—nuchal view, (**e**)—detail of dentition with measurements on P4, M1, and M2. Craniometric elements (A: akrokranion, B: basion, Ec: ectorbitale, En: entorbitale, Fm: frontal midpoint, N: nasion, O: opisthion, Ot: otion, P: prosthion, Po: palatinoorale, S: synsphenion, St: staphylion, Z: zygion) and measured parameters are as follows. In dorsal view, 1: total length, 2: zygomatic breadth, 3: greatest neurocranium breadth, 4: least breadth of the skull, 5: frontal breadth, 6: least breadth between the orbits, 7: viscerocranium length, 8: cranial length, 9: facial length; in lateral view, 10: skull height, 11: skull height without the sagittal crest, 12: neurocranium length, 13: greatest inner height of the orbit; in basal view, 14: condylobasal length, 15: basal length, 16: basifacial axis, 17: basicranial axis, 18: median palatal length, 19: palatal length, 20: length of the horizontal part of the palatine (from staphylion to palatinoorale), 21: length of the horizontal part of the palatine (from choanae to palatinoorale), 22: greatest mastoid breadth, 23: breadth dorsal to the external auditory meatus, 24: greatest diameter of the auditory bulla, 25: greatest palatal breadth, 26: length of the premolar row, 27: length of the molar row, 28: length of cheek tooth row; in nuchal view, 29: height of the foramen magnum, 30: height of the occipital triangle, 31: greatest breadth of the bases of the paraoccipital processes, 32: greatest breadth of the occipital condyles, 33: greatest breath of the foramen magnum; on teeth: GB (greatest breadth) only on P4 (fourth premolar), B (breadth) on P4, M1 (first molar) and M2 (second molar), L (length) on P4, M1 and M2.

3. Results

3.1. Order Proboscidea Illiger, 1811; Family Elephantidae Gray, 1821; Genus Mammuthus Brookes, 1828

Mammuthus primigenius (Blumenbach, 1799)

Material. One upper left last deciduous premolar (dP4 sin.), one tusk fragment (I^2), one fragment of undetermined long bone.

Measurements. Deciduous premolar has the following measurement values (in mm): length = –82.5–, width = ~58.5, height = 45 (buccal), 41 (lingual), enamel thickness = 1.5, number of lamellae = –7–. A dash, "–", indicates a missing/broken part of the tooth, thus the value is smaller than it would be on the complete specimen.

Description. The premolar is small, and the crown is partly damaged due to the sedimentation and transport processes. Part of the posterior root is preserved (Figure 3b,c). Dentin and cementum are light in color, while the enamel is darker, grey, and moderately folded. The lamellae are worn off almost to the bases. The height is greater on the buccal side of the crown. In the buccal and lingual views, the crown shows a convex shape of the occlusal surface line (anteroposteriorly). Thus, in spite of the somewhat concave occlusal surface in the mid-part, the premolar was determined to be maxillary. The shape of the lamellae is typical for the woolly mammoths: narrow cementum intervals and dentine parts. The dentine of the first and last two preserved lamellae is confluent due to chewing processes.

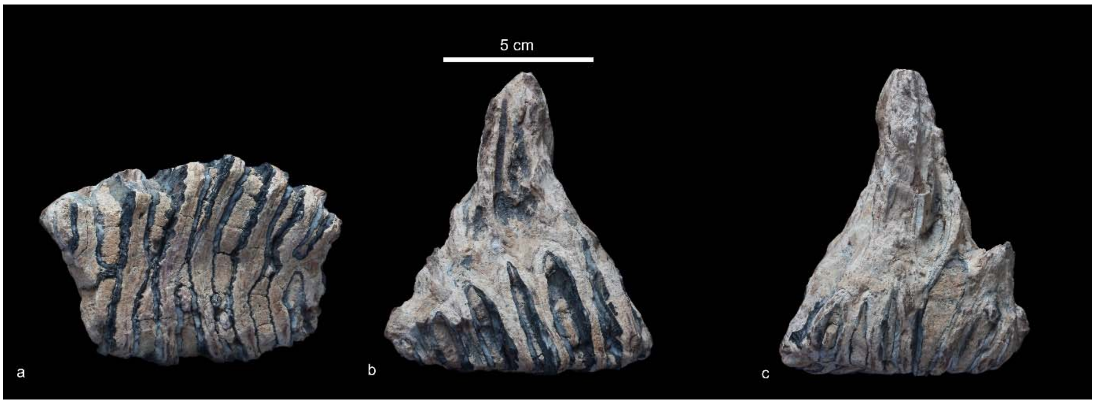

Figure 3. Last upper left deciduous premolar (dP4 sin.) of *Mammuthus primigenius* from the Sekuline site near Molve (Podravina region, NE Croatia): (**a**) occlusal surface, (**b**) buccal, (**c**) lingual side.

General remarks. Woolly mammoth is represented by three elements, of which two (tusk and long bone fragments) were used for radiocarbon dating and damaged during the analysis (thus, they were not available for the paleontological analyses). The last deciduous premolar obviously belonged to the woolly mammoth, based on the characteristic enamel pattern on the occlusal surface (Figure 3a), lamellae thickness, and other metric and morphologic features. The other found fragments also belong to the proboscideans, likely the woolly mammoth, whose remains are the most frequent finds on the territory of present-day Croatia compared to other proboscidean taxa. Radiometric dating results also support ascription of these remains to the woolly mammoth (see below).

Radiometric datings. Radiocarbon (^{14}C) ages for the woolly mammoth finds are: (a) bone fragment: conventional age is 30,700 ± 800 yr BP, and median age is 35,394 cal yr BP (analysis number: Z–4858); (b) tusk fragment: conventional age is 23,700 ± 3200 yr BP, and median age is 29,869 cal yr BP (analysis number: Z–4859). The latter result is less accurate due to the low amount of collagen.

3.2. Order Carnivora Bowdich (1821); Family Canidae Fischer von Waldheim, 1817; Genus Canis Linnaeus, 1758

Canis familiaris Linnaeus, 1758

Material. One skull with P3–4 sin. and dext., and M1–2 sin. and dext.

Measurements. Measurements (in mm) are given in Table 1, and craniometric indices/ratios are in Table 2.

Description. The *Canis familiaris* skull is very well preserved, with left and right third and fourth premolars (P3–4 sin. and dext.) and left and right first and second molars (M1–2 sin. and dext.) (Figures 4a–d and 5a–c). Incisors, canines, and the first two premolars are missing on both sides of the maxilla, as are both *ossa nasali*. On the left alveolar raw, a small fragment of the anterior root of P2 is visible in the alveola, while the posterior part of the P2 alveola is obliterated. On some parts, post-mortem damages to the bones are visible as well, for example, on left side of the maxillar bone, right zygomatic bone, left *bulla tympanica*, etc. On the right side of the maxillar bone, one abscess scar is present (Figure 5b,c), and transformed bone tissue can be observed, respectively. Due to the transport processes in the sediments, enamel has broken off from some places on the crowns.

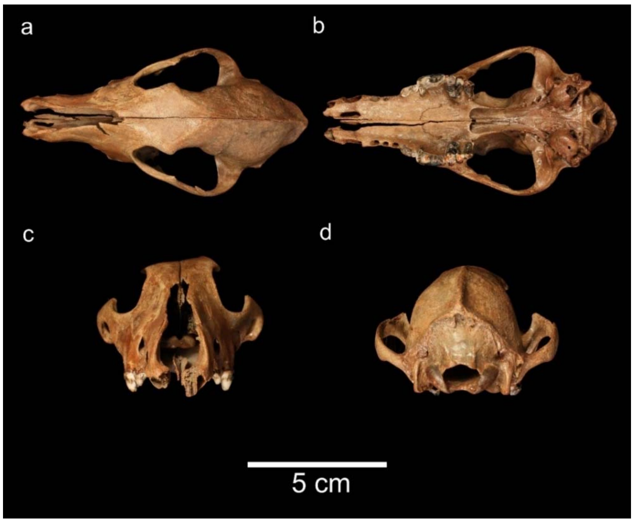

Figure 4. *Canis familiaris* skull from the Sekuline site: (**a**) dorsal, (**b**) basal, (**c**) anterior, (**d**) nuchal view.

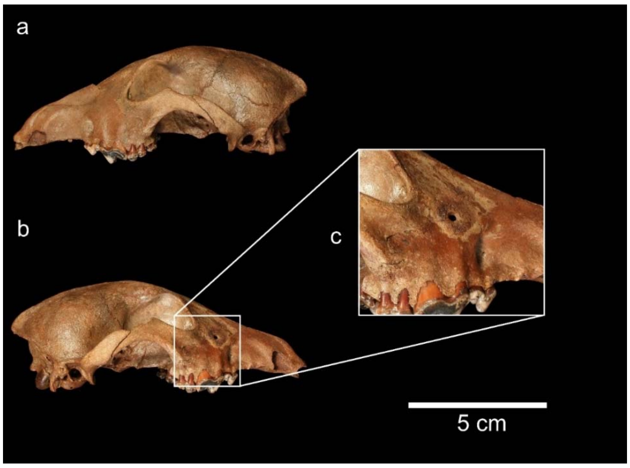

Figure 5. *Canis familiaris* skull from the Sekuline site: (**a**) lateral (left), (**b**) lateral (right) view, (**c**) detail with abscess scar on the maxillar bone.

Table 1. Measurements (mm) of different Croatian canid skulls: *Canis familiaris* from Sekuline near Molve and Vučedol sites, *C. aureus* from Slavonia, and *C. lupus* (female) from the Lika region. For four skulls (Inventory signature: Lx, L Mi, L, L 67) from the Early Bronze Age site in Vučedol (Eastern Slavonia), minimum to maximum parameter values are presented after Mihelić et al. [8]. For abbreviations, see Figure 2.

Taxa	Locality	1	2	3	4	5	6	7	8	9	10
Canis familiaris	Sekuline	194.6	98.5	54.0	34.8	45.2	35.5	99.0	94.0	117.4	55.0
Canis familiaris	Vučedol	151–191	94–104	52–54	-	49–55	35–38	75–99	73–91	83–110	-
Canis aureus	Slavonia	177.3	95.9	55.4	28.5	45.0	27.3	85.4	83.5	100.0	52.5
Canis lupus (♀)	Lika	213.3	113.5	66.5	40.5	53.1	40.0	106	98.0	123.0	61.8
Taxa	**Locality**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Canis familiaris	Sekuline	48.0	101.8	28.3	177.7	170.5	125.4	47.1	94.9	93.0	33.2
Canis familiaris	Vučedol	-	80–101	26–30	148–186	139–174	-	-	-	-	-
Canis aureus	Slavonia	48.0	92.5	30.0	166.0	155.0	111.0	46.2	83.2	81.8	33.0
Canis lupus (♀)	Lika	56.5	110.0	33.0	204.5	194.0	141.0	53.3	104.5	103.8	37.1
Taxa	**Locality**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Canis familiaris	Sekuline	31.3	60.8	61.0	20.0	57.9	50.5	20.0	67.5	15.1	43.0
Canis familiaris	Vučedol	-	56–69	-	-	-	-	-	-	14–16	37–40
Canis aureus	Slavonia	31.6	60.6	58.5	25.9	55.2	46.8	19.6	62.5	14.5	40.0
Canis lupus (♀)	Lika	36.4	73.5	71.0	28.0	71.6	56.0	21.5	73.0	17.0	51.0
Taxa	**Locality**	**31**	**32**	**33**							
Canis familiaris	Sekuline	50.2	35.5	18.5							
Canis familiaris	Vučedol	45–53	34–37	18–19							
Canis aureus	Slavonia	47.5	33.2	18.4							
Canis lupus (♀)	Lika	60.0	44.0	22.2							
Taxa	**Locality**	**GB (P4)**	**B (P4)**	**B (M1)**	**B (M2)**	**L (P4)**	**L (M1)**	**L (M2)**			
Canis familiaris	Sekuline	11.5	8.7	14.6	10.3	19.5	12.5	8.0			
Canis aureus	Slavonia	9.4	6.4	13.5	9.6	17.0	12.2	7.5			
Canis lupus (♀)	Lika	12.5	9.8	17.5	10.8	22.5	15.0	8.5			

Table 2. Craniometric indices and ratios for *Canis familiaris* skulls from Sekuline and Vučedol sites. For four skulls (Inventory signatures: Lx, L Mi, L, L 67) from the Early Bronze Age site in Vučedol (Eastern Slavonia), minimum to maximum values are presented after Mihelić et al. [8].

Locality	Skull Index 2/1 × 100	Cranial Index 3/NA × 100	Facial Index 2/7 × 100	Foramen Magnum Index 29/33 × 100	Length–Length Index 2 NA/7	Ratio of Cranium to Facial Bones NA/7 × 100
Sekuline	50.62	49.09	99.49	81.62	1.11	111.11
Vučedol	54.25–62.25	51.49–67.50	105.05–125.33	73.68–88.89	1.02–1.08	102.02–108.23

General remarks. The abscess scar is the result of infection, which very often appears in dogs' mouths around the roots of the fourth upper premolars (P4), which are the largest of dogs' dentitions and are also called the carnassial teeth (as are the first lower molars). They are massive three-rooted teeth with long roots that are used by the dogs to crack bones [10,11]. The roots are so long that they reach into the maxillary sinuses, upon which the abscess later forms, likely caused by chewing heavy bones, which can result in cracking or fracturing the enamel of the teeth. These infections allow bacteria to migrate from the root into the maxillary bone that forms the face and maxillary sinus. The injury was not lethal in the presented specimen from Sekuline, and the animal lived for some time after, with changes to the bone tissue around the wound. Furthermore, the loss of alveolar bone around the roots on both sides is likely a result of periodontal disease.

Some of the palatal, maxillar, and zygomatic bones are partly disconnected due to the drying/fossilization processes. All permanent teeth are erupted, with slight traces of wear on the occlusal surfaces; thus, the approximate age at the time of death of the specimen could be around 5 years or more [12].

Based on the values of craniometric indices and ratios, it is concluded that the Sekuline skull is dolichocephalic (Table 2).

3.3. Order Artiodactyla Owen, 1848; Family Cervidae Goldfuss, 1820

3.3.1. Genus *Megaloceros* Brookes, 1828; *Megaloceros giganteus* (Blumenbach, 1799)

Material. One fragment of the right antler, one atlas, and the proximal half of a metacarpal bone.

Measurements (in mm). Atlas: breadth of the *facies articularis cranialis* = 98.5;

metacarpus: breadth of the proximal end = 62.3, depth of the proximal end = 44.0.

Description. The antler is preserved, with the most basal portion of the beam growing from a bony pedicle, indicating that the antler was still attached to the skull at the time of the animal's death (Figure 6). The coronet is heavily abraded and barely visible, while the brow tine is broken off at its base. The surface shows traces of weathering in the form of deep longitudinal fractures and moderate spalling, in addition to severe abrasion. Edges around the superior end of the beam portion are rugged and discoloured, undoubtedly originating recently. Unfortunately, the remaining parts of this antler were not found.

The atlas consists of both ventral and dorsal arches (Figure 6). The cranial side has its joint facets preserved, while the caudal side is damaged and partially missing. The whole specimen is heavily abraded, exposing the inner cancellous structure of bone. In addition, both transverse processus are largely reduced.

The proximal half of the left metacarpal bone retained its morphological features but has numerous fine-line fractures with moderate surface spalling, especially on its posterior side (Figure 6). The distal portion is broken off and missing, so it is not possible to assert the relative age of the individual.

General remarks. All three fragments identified as a giant deer are heavily weathered and abraded; the colour is pale brown on the surface and dark brown in the cortex, indicating stronger mineralisation. Generally, these fragments passed through more pronounced diagenetic processes than the red deer bones (see Section 3.3.2.), suggesting a greater difference in the time of deposition (i.e., much older material). Although it cannot be confirmed, the size and taphonomy of these specimens imply the possibility that all could come from the same individual.

Figure 6. *Megaloceros giganteus* remains from the Sekuline site (from left to right): fragment of the right antler; atlas, dorsal view; proximal part of the left metacarpus (Mc sin.), anterior view.

3.3.2. Genus *Cervus* Linnaeus, 1758; *Cervus elaphus* Linnaeus, 1758

Material. One cranial fragment with the left antler, one right maxilla with all cheek teeth (P2–M3), one complete right tibia.

Measurements (in mm). Cranium: basicranial axis = 90.5, greatest breadth of the occipital condyles = 85.4, greatest breadth of the bases of the paraoccipital processes = 136.2, greatest breadth of the foramen magnum = 33.7, proximal circumference of the burr (circumference of the distal end of the pedicel) = 227.3;

maxilla: length of the cheek tooth raw = 122.4, length of the molar raw = 71.6, length of the premolar raw = 49.3;

upper teeth: see Table 3.

Table 3. Measurements (length = L, breadth = B) of the third and fourth premolars (P3, P4), and first, second, and third molars (M1, M2, M3) of *Cervus elaphus* from the Sekuline site.

Measurements (occlusal)/Teeth	P3	P4	M1	M2	M3
L	18.4	17.0	21.8	26.4	27.7
B	15.0	17.2	19.4	22.4	21.7

tibia: greatest length = 420.0, breadth of the proximal end = 87.4, depth of the proximal end = 87.4, smallest breadth of the diaphysis = 34.9, breadth of the distal end = 57.1, depth of the distal end = 44.8.

Description. The fragment of the cranium with an antler (Figure 7) belonged to an adult buck and consists of the uppermost, caudal, and basal cranial parts, including almost complete frontal, parietal, occipital, and temporal paired bones, as well as pterygoid and sphenoid. The facial bones are all missing. The frontal bones are nearly complete with both orbits, supraorbital foramina, and pedicles. The right-side frontal end towards the nasal bones is broken off. Both parietal bones are complete. Occipital bones are also complete, except for slightly eroded edges of paracondylar processus. Both zygomatic arches are broken and only partially preserved. The uppermost part of the skull has a complete left antler attached to the pedicle, while the right bony pedicle is broken off just below the base of the missing antler. The left antler has a completely preserved beam with the coronet and six tines. The coronet surrounding the pedicle near the base of the antler has knobbly lumps. Irregular grooves running along the length of the beam and tines are very pronounced, while the tips of the tines are quite smooth due to use while the animal was alive. All these features show no temporal decay, indicating a relatively recent age of this specimen. In addition, the cranial bone surface shows very light spalling and the texture of the antler is almost perfectly preserved, both indicating relatively minimum to no post-depositional disturbances of this specimen.

The right maxilla is almost complete. The alveolar process has just a small portion broken off below the infraorbital foramen, exposing the dental alveolus of the second premolar. Both posterior and medial ends are damaged, with the zygomatic and palatal processus partially missing, respectively. The frontal end is perfectly preserved, with an unfused suture towards the missing premaxilla. The dental arch is complete, with all cheek teeth still inside the alveoli, while the upper canine is missing. Preserved teeth are unbroken and fully erupted, with moderately worn occlusal surfaces (Figure 7, Table 3). The aforementioned cranium and this maxilla are almost identical in size and surface taphonomy, and most likely belonged to the same skull.

The complete right tibia has both epiphyses fully fused. The bone is dark brown in colour and the surface texture is very smooth. Oblique, very shallow, and wide scrapings on the anterior side of distal portion of the diaphysis are the only bone modifications visible and may have been caused by abrasion due to natural post-depositional processes. Generally, this tibia is very well preserved and is probably subrecent to recent.

Figure 7. *Cervus elaphus* remains from the Sekuline site (from left to right): cranium with left antler; right maxilla with teeth; right tibia, anterior view.

General remarks. All red deer specimens are darker in colour, having yellowish brown to dark brown staining and discolouration, indicating partial mineralisation, probably due to being exposed to waterlogged deposits [13]. In addition to being complete or mostly preserved, all three specimens show no or only minor surface weathering (e.g., spalling on maxilla), indicating favourable preservation conditions and relative recency in comparison to other associated animal remains.

Generally, the size, age, and taphonomy of all fragments identified as red deer show great similarities and may be used as a strong indicator that their possible origin is from a single individual. Since the antler is full-grown and unshed, this red deer individual died sometime in autumn or winter [14]. Fused cranial sutures indicate an adult, while the two fused tibia epiphyses and dental wear suggest a relative age of at least 2.5 years [15,16].

4. Discussion

4.1. *Mammuthus primigenius*

During the Late Pleistocene, the woolly mammoths were widely distributed all over Eurasia, especially in the central and northern regions. Periodically, their areal extent decreased, for example, in the Huneborg stadial (36–33 ka BP) [15], when they were distributed more southwards. During the

Denekamp interstadial (33 to ~24 ka BP), they were again widespread all over Eurasia [17]. The oscillations in their distribution/areal extent followed the climate fluctuations and changes in vegetation during the Late Pleistocene. Their skeletal remains have been found across a geographically vast area that includes the Iberian Peninsula, Germany, the British Isles, the northern and northeastern parts of Eastern Europe, and other countries. Stuart and co-authors [18] reported that the latest dates for the mammoth bones from the Italian Settepolesini site near Ferrara are in the range of 35.8–33.83 ka BP. The results of dating for the woolly mammoths from the Hungarian localities show that the most common age of MIS 2 mammoths is between 24.1 and 21.8 ka BP [19]. Kovács [20] reported the youngest radiometric age to be 16.7–15.8 ka BP for the Hungarian woolly mammoth from the Csajág site. Furthermore, the same author presumed that the woolly mammoths completely disappeared from the Hungarian part of the Pannonian basin approximately 16 ka BP. It can be concluded that the mammoth's geographical distribution was the greatest before the Last Glacial Maximum, around 28–24 ka BP [17]. Climate (for example, increase of humidity and thickness of the snow cover) and environmental changes (degradation of mammoth steppe, disappearance of open periglacial landscapes) at the end of the Late Pleistocene and beginning of the Holocene caused the rapid extinction of the woolly mammoths [17], with the possible influence of the hunting strategies of the Late Palaeolithic and Mesolithic hominins.

Woolly mammoth remains have been reported from many Croatian localities, most of which originate from the sites along the biggest rivers in the country: Sava, Drava, and Dunav (Danube), as well as their tributaries [4]. The absolute age of the mammoth finds from Croatia was not known until now, but it was presumed that they lived in this region at the same time, which was proved for this species from neighboring countries.

4.2. *Canis familiaris*

Thalmann and co-authors [21] reported that the mitochondrial genomes of all modern dogs are phylogenetically most closely related to either ancient or modern canids of Europe. Furthermore, these authors proposed Middle East and East Asia as the centers of dog origin and argued that the domestication processes occurred between 32.1 and 18.8 ka BP. Thus, the domestication of the wolves preceded the Neolithic (time of agriculture) and occurred within the European Upper Palaeolithic hunter-gatherer groups [22]. The oldest dog remains found in Western Europe and Siberia were dated from 36 to 15 ka BP, and the oldest finds from the Middle East and East Asia are not older than around 13 ka BP [21]. One of the oldest prehistoric dogs is the well-known specimen from Goyet in Belgium, dated to ca. 31.7 ka BP [23], and it resembles the prehistoric dogs more than it resembles the recent wolves. The same authors concluded that, between 14 and 10 ka BP, dogs were present at different sites in Europe and Asia.

It is well-known that dogs became domesticated from wolves. The specific determination is not easy, since the morphology of these two taxa is very similar. Metrical differences are more prominent, but accurate taxonomic determination is not always possible, although metrical values differ to some extent.

Although dogs are common animals, they are not often reported from fossil and/or recent localities.

The find from Sekuline shows a peculiar abscess scar on the maxillar bone, which is, so far, the first mention of such a case on a dog skull from a Croatian locality. In comparison to the Vučedol dog skulls, the Sekuline specimen shows both similarities and differences. The profile forehead line is straighter in the Sekuline dog than in modern dogs, and it is similar to the shape of a golden jackal and a wolf. From the overall morphometric results (see Table 1), the dog from Sekuline has a skull size that is smaller than the wolf's, and it is quite similar in most dimensions to the jackal skull, which is slightly smaller (Figure 8a–c).

Germonpré and co-authors [22] stated that "the overall cranial size of the Palaeolithic dog morphotype is significantly smaller than that of the Pleistocene wolves. Most researches agree that the early stages in process of domestication are accompanied by a decrease in body size with respect to the wild ancestor and that a universality of body size diminution under anthropogenic environments exists". Furthermore, the same authors [22] mentioned that the "muzzle of the Palaeolithic dogs was on average shorter and relatively wider than that of the Pleistocene wolves. The shortening of the facial part of the skull is considered typical of domestication in mammals"; this is defined in literature as "domestication syndrome". The research provided by O'Keefe et al. (cited from [22]) shows that the skull morphology of the recent North American wolf depends on prey availability; thus, a decreasing size of the skulls could be correlated with smaller prey animals.

Figure 8. Comparison of the canid skulls: (**a**) *Canis lupus* (female) from the Lika region; (**b**) *C. familiaris* from the Sekuline site; (**c**) *C. aureus* from the Slavonia region.

In addition, the carnassial crown length is proved not to differ significantly between wolves and Palaeolithic dogs, although, in dogs, these values are slightly smaller than in Pleistocene and recent Northern wolves, respectively.

4.3. *Megaloceros giganteus*

The family *Cervidae* evolved in Eurasia during the early Miocene [24,25] and were abundantly present during the Pleistocene in Europe.

Megaloceros giganteus appeared in Europe before approximately 400 ka BP and went extinct about 8000 years ago. These animals lived in Eurasia [24], from Ireland to central Siberia. They were the largest known members among cervids, with a shoulder height of 2 m and antlers reaching up to 3.5–4 m. Because of these enormous antlers, it is presumed that the giant deer were animals of open landscapes [26]. Phylogenetic analysis, which included morphological and aDNA sequence data, proved that the giant deer is a sister group of the fallow deer (*Dama dama*) [27].

The genus *Megaloceros* is also known from Croatian sites, for example, the Vindija cave [28,29] and Hijenska cave [30].

4.4. *Cervus elaphus*

The deer evolved from the ruminants living during the Miocene [24]. *Cervus elaphus* is well known from fossil sites, cave drawings, and the recent faunal list from many localities, and it was a common species during the Pleistocene, especially during the Late Pleistocene of Europe. Today, the species has a wide distribution and inhabits large deciduous and mixed forests [31], from Eurasia and northern Africa to North America, respectively.

5. Conclusions

The described faunal assemblage consists of Late Pleistocene and Holocene remains that clearly show different taphonomic histories. The remains of the recent taxa (dog and red deer) are well preserved with only minor surface weathering. The main taphonomic characteristic is their darker color, indicating exposure to a wet/waterlogged environment, but probably with very little to no post-depositional movement. On the contrary, the remains of the fossil taxa (mammoth and giant deer) are quite damaged, fragmented, heavily weathered, and their color suggests marked diagenetic changes, i.e., all of these factors indicate much longer depositional history with transport processes. Generally, the taxonomic and taphonomic composition of these remains suggests the undoubtedly allochthonous character of this assemblage, and such finds are relatively common in Croatian fluvial Late Pleistocene and Holocene sediments.

Although the allochthonous material does not provide enough information about its origin and/or stratigraphy of the site, it has value. The described faunal representatives can fill gaps in the overall reconstruction of the faunal, climatic, and environmental conditions in the Drava river area during the Late Pleistocene and Holocene.

The results of radiocarbon dating of the woolly mammoth remains from Croatia are concordant with those from the neighboring countries, such as Hungary [19] and Italy [18]. It can be concluded that during the Huneborg stadial (36–33 ka BP) and Denekamp interstadial (33 to ~24 ka BP) in the northern and northeastern parts of present-day Croatia, which belong to a wider Pannonian basin, provided favorable habitats for the representatives of the so-called *Mammuthus-Coelodonta* Faunal Complex [26], or cold-adapted large mammals, in the material from Sekuline presented by woolly mammoth and giant deer. These are well-known animals from the mammoth-steppe, or steppe and forest-steppe environment, which was spread over particular areas of Eurasia during some intervals of the Late Pleistocene. As a forest animal of temperate climate, red deer are part of the recent fauna in many places in Croatia, but they can also be found in Late Pleistocene faunas. It was not possible to determine which breed the dog belonged to, but it definitely represents the recent animal, somewhat bigger than the golden jackal, which has spread recently (over the last 15–20 years) from the coastal parts and islands to the continental areas of Croatia (for example, Slavonia). It is also known from northeast parts of Italy [31]. On the other hand, the Sekuline dog skull is smaller than that of the female wolf specimen, which is in concordance with the data from other localities.

Future exploitation of the gravels in Sekuline lakes, as well as further radiometric dating, could provide more fossil and recent animal remains and help to better understand the fauna and environments of this area during different parts of the Quaternary.

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References

1. Panonska nizina. Hrvatska Enciklopedija; Leksikografski zavod Miroslav Krleža. Available online: http://www.enciklopedija.hr/natuknica.aspx?id=46451 (accessed on 20 July 2018).
2. Malez, M.; Brajković, D. Gornjopleistocenski sisavci u naplavinama rijeke Drave (Hrvatska) [Upper-Pleistocene mammals in alluvial deposits of the river Drava (Croatia)]. *Geol. Vjesn.* **1991**, *44*, 31–37, (In Croatian with English Summary).
3. Winkler, E.M.; Paunović, M. Ein menschlicher Unterkiefer aus den jungpleistozänen Ablagerungen der Drau bei Šašnato polje, Kroatien. *Mitt. Anthropol. Ges. Wien* **1992**, *122*, 109–153.
4. Mauch Lenardić, J. Miocene to Late Pleistocene proboscideans of Croatia. *Quat. Int.* **2012**, *276–277*, 120–128. [CrossRef]
5. Mauch Lenardić, J.; Oros Sršen, A.; Radović, S. Quaternary fauna of the Eastern Adriatic (Croatia) with the special review on the Late Pleistocene sites. *Quat. Int.* **2017**, in press. [CrossRef]
6. Von den Driesch, A. A guide to the measurement of animal bones from archaeological sites. *Bull. Peabody Mus. Nat. Hist.* **1976**, *1*, 1–137.
7. Zinoviev, A.V. Study of the Medieval Dogs from Novgorod, Russia (X–XIV Century). *Int. J. Osteoarchaeol.* **2012**, *22*, 145–157. [CrossRef]
8. Mihelić, D.; Pavić, M.; Hincak, Z. A Craniometrical Analysis of the Early Bronze Age Dogs from Vučedol Site (East Slavonia, Croatia). *Coll. Antropol.* **2013**, *37*, 239–244. [PubMed]
9. Horvatinčić, N.; Barešić, J.; Krajcar Bronić, I.; Obelić, B. Measurement of low ^{14}C activitie in a liquid scintillation counter in the Zagreb Radiocarbon Laboratory. *Radiocarbon* **2004**, *46*, 105–116. [CrossRef]
10. Naeini, A.T.; Jahromi, A.R.; Mehrshad, S. Bilateral abscesses of the maxillary carnassial teeth in a female Pekinese. *Turk. J. Vet. Anim. Sci.* **2010**, *34*, 461–464. [CrossRef]
11. Reiter, A.M. Endodontic Disease in Small Animals. Available online: https://www.msdvetmanual.com/digestive-system/dentistry/endodontic-disease-in-small-animals (accessed on 9 April 2018).
12. The Human Society of the United States. How to Determine a Cat's or Dog's Age. 1996. Available online: http://www.ruralareavet.org/PDF/Physical_Exam-How_to_Determine_Age.pdf (accessed on 23 May 2018).
13. Lyman, R.L. *Vertebrate Taphonomy. Cambridge Manuals in Archaeology*; Cambridge University Press: Cambridge, UK, 1999; pp. 1–524. ISBN 0-521-45840-4.
14. Schmid, E. *Atlas of Animal Bones. For Prehistorians, Archaeologists and Quaternary Geologists*; Elsevier Publishing Company: Amsterdam, The Netherlands, 1972; pp. 1–159. ISBN 0-444-40831-2.
15. Brown, W.A.B.; Chapman, N.G. The dentition of red deer (*Cervus elaphus*): A scoring scheme to assess age from wear of the permanent molariform teeth. *J. Zool.* **1991**, *224*, 519–536. [CrossRef]
16. Reitz, E.J.; Wing, E.S. *Zooarchaeology. Cambridge Manuals in Archaeology*; Cambridge University Press: Cambridge, UK, 1999; pp. 1–455. ISBN 0-521-48529-0.
17. Markova, A.K.; Puzachenko, A.Y.; van Kolfschoten, T.; van der Plicht, J.; Ponomarev, D.V. New data on changes in the European distribution of the mammoth and the woolly rhinoceros during the second half of the Late Pleistocene and the early Holocene. *Quat. Int.* **2013**, *292*, 4–14. [CrossRef]
18. Stuart, A.J.; Sulerzhitsky, L.D.; Orlova, L.A.; Kuzmin, Y.V.; Lister, A.M. The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. *Quat. Sci. Rev.* **2002**, *21*, 1559–1569. [CrossRef]
19. Konrád, G.; Kovács, J.; Halász, A.; Sebe, K.; Pálffy, H. Late Quaternary woolly mammoth (*Mammuthus primigenius* Blum) remains from southern Transdanubia, Hungary. *C. R. Palevol.* **2010**, *9*, 47–54. [CrossRef]
20. Kovács, J. Radiocarbon chronology of Late Pleistocene large mammal faunas from the Pannonian basin (Hungary). *Bull. Geosci.* **2011**, *87*, 13–19. [CrossRef]
21. Thalmann, O.; Shapiro, B.; Cui, P.; Schuenemann, V.J.; Sawyer, S.K.; Greenfield, D.L.; Germonpré, M.B.; Sablin, M.V.; López-Giráldez, F.; Domingo-Roura, X.; et al. Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science* **2013**, *342*, 871–874. [CrossRef] [PubMed]

22. Germonpré, M.; Fedorov, S.; Danilov, P.; Galeta, P.; Jimenez, E.-L.; Sablin, M.; Losey, R.J. Palaeolithic and prehistoric dogs and Pleistocene wolves from Yakutia: Identification of isolated skulls. *J. Archaeol. Sci.* **2017**, *78*, 1–19. [CrossRef]
23. Germonpré, M.; Sablin, M.V.; Stevens, R.E.; Hedges, R.E.M.; Hofreiter, M.; Stiller, M.; Després, V.R. Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. *J. Archaeol. Sci.* **2009**, *36*, 473–490. [CrossRef]
24. Kurtén, B. *Pleistocene Mammals of Europe*; Library of Congress Catalog Card Number 68-29953; Aldine Publishing Company: Chicago, IL, USA; G. Weidenfeld & Nicolson Ltd.: London, UK, 1968; pp. 1–317.
25. Valli, A.M.F. Late Pleistocene Deer in the Region of the National Park "Serra da Capivara" (Piauí, Brazil). *Quaternary* **2018**, *1*, 4. [CrossRef]
26. Kahlke, R.-D. *The History of the Origins, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (Large Mammals)*; Fenske Companies: Rapid City, SD, USA, 1999; pp. 1–219. ISBN 0-913062-04-9.
27. Lister, A.M.; Edwards, C.J.; Nock, D.A.W.; Bunce, M.; van Pijlen, I.A.; Bradley, D.G.; Thomas, M.G.; Barnes, I. The phylogenetic position of the "giant deer" *Megaloceros giganteus*. *Nature* **2005**, *438*, 850–853. [CrossRef] [PubMed]
28. Malez, M.; Rukavina, D. Položaj naslaga spilje Vindije u sustavu članjenja kvartara šireg područja Alpa (Lage der Höhlenablagerungen von Vindija im System der quartären Vollgliederung des Alpengebietes). *Rad JAZU* **1979**, *383*, 187–218, (In Croatian with German summary).
29. Miracle, P.T.; Mauch Lenardić, J.; Brajković, D. Last glacial climates, "Refugia", and faunal change in Southeastern Europe: Mammalian assemblages from Veternica, Velika pećina, and Vindija caves (Croatia). *Quat. Int.* **2010**, *212*, 137–148. [CrossRef]
30. Malez, M. Hijenske pećine u doba Pleistocena na području Hrvatske (Hyänenhöhlen aus dem Pleistozän in Kroatien). *Rad JAZU* **1975**, *371*, 307–316, (In Croatian with German summary).
31. Aulagnier, S.; Haffner, P.; Mitchell-Jones, A.J.; Moutou, F.; Zima, J. *Mammals of Europe, North Africa and the Middle East*; A&C Black Publishers Ltd.: London, UK, 2008; pp. 1–272. ISBN 978-1-4081-1399-8.