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Craniometric characteristics of the water deer *Hydropotes inermis* (Swinhoe 1870) from a new population in the southern Russian far eastValeriya Omelko^{1,*}, Yury Darman^{2,3}, Gleb Sedash⁴¹ Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690022, Russia² Pacific Geographical Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690041, Russia³ Federal State Budgetary Institution Joint Directorate of Kedrovaya Pad' State Biosphere Nature Reserve and Land of the Leopard National Park, Vladivostok, Russia⁴ Ilbirs Foundation Public Fund, Bishkek, Kyrgyz Republic

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ABSTRACT

The aim of this study was to obtain craniometric characteristics of the water deer *Hydropotes inermis* (Swinhoe, 1870) from a newly established population in the Russian Federation and to compare them with those of water deer from Central China and South Korea, as well as with those of the Siberian roe deer and the musk deer. In total, 50 cranial and mandibular measurements were recorded. A comparison with populations from Central China and South Korea revealed that deer from the Russian population are significantly larger in key craniometric parameters. We documented the developmental stages of male and female canines. Craniometric distinctions between the water deer, Siberian roe deer, and musk deer are also demonstrated.

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Introduction

The water deer (*Hydropotes inermis* Swinhoe 1870) once inhabited all the coastal plains surrounding the Yellow Sea (Whitehead 1993). Today, only two isolated populations remain (Figure 1). The subspecies *H. i. inermis* Swinhoe 1870—the Chinese water deer—inhabits the lower Yangtze River basin in central China. The subspecies *H. i. argyropus* Heude, 1884—the Korean water deer—occurs on the Korean Peninsula, primarily in the marshy lowlands of the western coast (Harris and Duckworth 2015). In recent years, the water deer has expanded its range northward by at least 500 km beyond its former distribution, now occurring in the southern Russian Far East and southeastern Jilin Province of China (Darman et al. 2019; Li et al. 2022; Li et al. 2023).

In the Russian Federation, the water deer was officially recorded for the first time in 2019 in Primorsky Krai, within the “Land of the Leopard” National Park. A distinctive feature of male water deer is their long, curved, sabre-like canines, and the absence of

antlers. Because of this, local residents of the Khasansky District, who first observed the species around ten years ago, mistakenly identified it as a “marsh musk deer”. The species is actively spreading from the Tumannaya (Tumangan) River to the middle reaches of the Razdolnaya River, favoring marshy coastal lowlands with shallow lakes, broad river floodplains with reed swamps, shrub thickets, and wet meadows. According to aerial surveys, the population grew from 170 to 300 individuals between 2019 and 2022 (Darman and Sedash 2020; Petrov et al. 2025).

General descriptions of the water deer skull compared to other cervids and the musk deer date back to the 19th century (Swinhoe 1870; Brooke 1872; Rüttimeyer 1881). Distinctive features of the skull include small orbits, small lacrimal pits on the lacrimal bones with two lacrimal ducts and a cribriform slit, and the absence of supraorbital processes. The supraorbital foramen lies in a depression, and the occipital bone is narrow and slightly ridged. Characteristic features of the water deer include an elongated groove around the supraorbital foramen and the absence of supraorbital ridges (Schilling and Rossner 2017). However, we found only a few studies on craniometrics analyses of water deer from different native populations. All of them were conducted by Kim Yung Kun from Seoul National University (Kim et al. 2013, Kim et al. 2015). He used the skull collections from East China Normal University, the Shanghai Science and Technology Museum,

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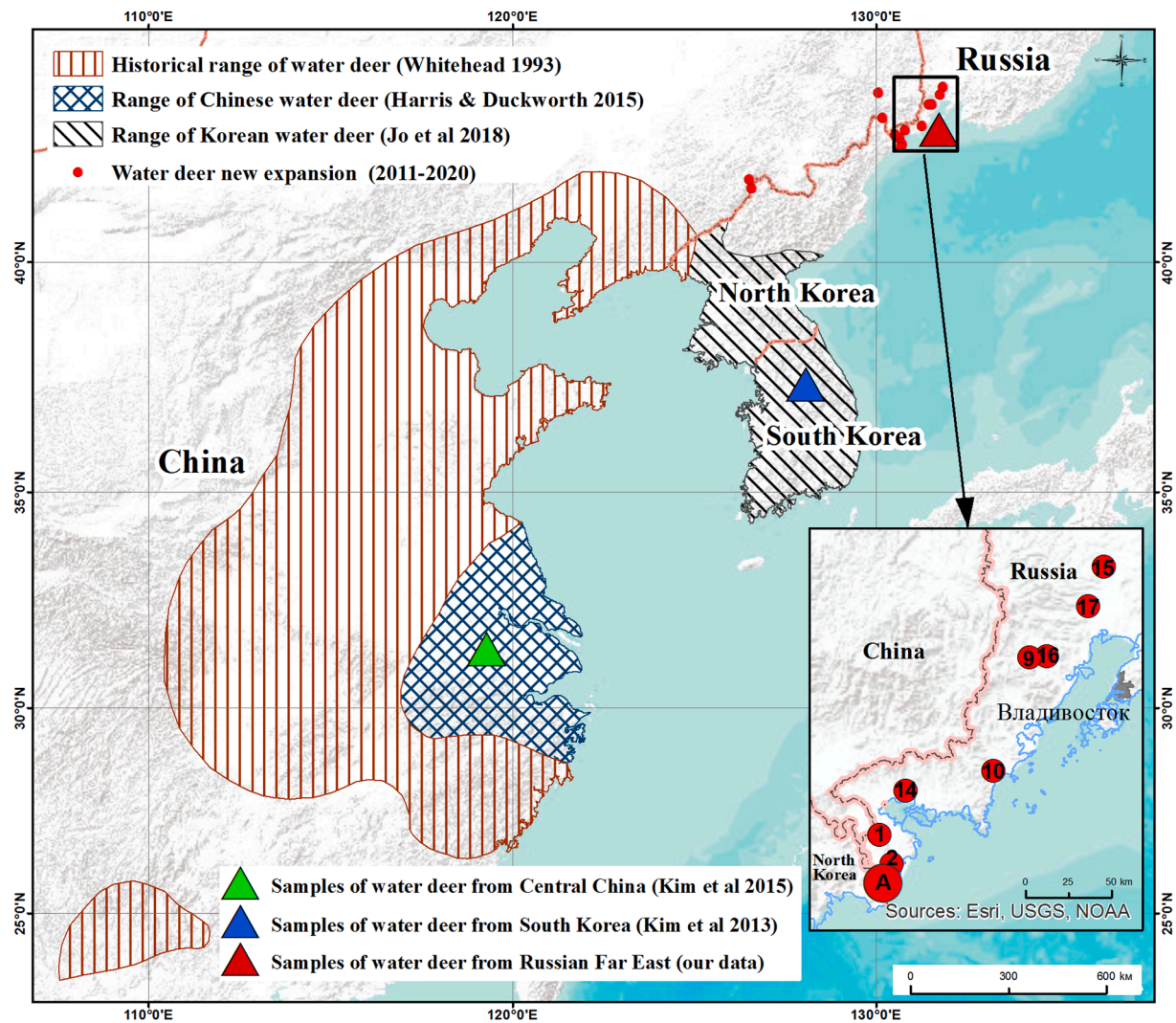


Figure 1. Distribution of the water deer in East Asia. Red numbered circles indicate the collection localities of specimens included in this study, with their corresponding collection numbers provided in [Appendix A](#). Circles marked with "A" denote the collection localities of specimens Nos. 3, 4, 5, 7, 8, 12, and 13.

and the Chinese Academy of Sciences, Beijing (30 adult males)). For the Korean water deer, all specimens were collected by the Conservation Genome Resource Bank for Korean Wildlife and kept in the Department of Anatomy and Cell Biology, College of Veterinary Medicine, Seoul National University (28 adult males).

Due to the recent appearance of the water deer in Russia, its morphology in this region remains poorly studied. The first craniometric data in Russia were obtained by us based on measurements of five skulls ([Darman et al. 2022](#)). Another publication provided only external measurements based on a single individual ([Fomenko et al. 2022](#)). There is only one publication in Russia that addresses morphotypic differences between water deer skulls and those of other small wild and domestic ungulates in Primorye ([Belyaev et al. 2023](#)). However, detailed morphometric comparisons for the Russian Far East have not yet been conducted. Such data are especially important for field studies and for the identification of paleontological remains. Therefore, the aim of this study was to obtain craniometric characteristics of water deer from a newly established population in the Russian Federation and to compare them with those of water deer from Central China and South Korea, as well as with those of roe deer and musk deer.

Material and methods

This study is based on a collection of 15 water deer skulls obtained from individuals that died at different times due to poaching, predation, or vehicle collisions in the Khasansky District of Primorsky Krai, Russia, between $N42^{\circ}20'14''-43^{\circ}35'22''$ and $E130^{\circ}26'6''-131^{\circ}51'32''$ ([Appendix A](#)).

Following [Kim et al. \(2013\)](#), we categorized the specimens into four age groups based on the eruption and wear status of the molars:

- Group I: M1 fully erupted
- Group II (5–6 months): M1 and M2 fully erupted
- Group III (10–12 months): M1, M2, and M3 fully erupted
- Group IV: M1, M2, and M3 fully erupted and worn

However, the exact age of individuals in each group is not always known, as no established method currently exists for age determination in water deer. Observations in captivity have shown that the second molar erupts at around 5–6 months of age, and the third molar at around 10–12 months ([Cooke 2019](#)).

Among the skulls examined, the estimated ages were as follows: one male skull was categorized as Group I–II, three as Group II, one as Group II–III, six as Group III, and one as Group IV. Two female skulls were assigned to Group II and one to Group III (Appendix B).

In addition to the standard skull measurement scheme for cervids (Danilkin 1999), we applied additional measurements used by the Korean researchers (Kim et al. 2013; Kim et al. 2015) (Figure 2). We also measured the lengths of the upper and lower molar rows and the canines. In total, 50 cranial and mandibular measurements were recorded. Measurements were taken using calipers with an accuracy of 1 mm. Full measurement data for each skull are provided in Appendix B.

For the most numerous subset—males from Groups III and IV ($n = 8$)—mean values were calculated and used as the basis for comparative analysis with existing craniometric data for water deer from South Korea and Central China (Kim et al. 2013; Kim et al. 2015). To assess the significance of differences between measurements, we applied a two-tailed one-sample Student's t -test. Prior to hypothesis testing, the distribution of the data was evaluated using the Shapiro–Wilk test. However, given the small sample sizes (≤ 8) and the presence of repeated values, the power of normality tests is limited and the results should be interpreted with caution. Morphometric data of this type are commonly treated as approximately normally distributed in similar studies (e.g. Kim et al. 2013; 2015). All analyses were conducted in R, with the threshold for statistical significance set at $p < 0.05$.

Results and discussion

The average cranial measurements of adult male water deer from the southern Russian Far East, in comparison with data from South Korea and Central China, are presented in Table 1. Since no data on the mandibles of Chinese specimens were available in the literature, mandibular measurements were compared only with the Korean sample. Twelve cranial measurements were significantly larger than those of deer from Central China and fifteen than those from South Korea—on average by 6.4%—ranging from 3.5% to 13.2% (Table 1, bolded). For example, total skull length (TL) was significantly greater in the Russian sample than in Central China (175.0 mm vs. 169.2 mm; $p = 0.024$) and South Korea (175.0 mm vs. 168.3 mm; $p = 0.014$). Similarly, basal length (BL) was greater in Russia (154.0 mm) than in China (148.6 mm; $p = 0.013$) and Korea (147.8 mm; $p = 0.007$). These measurements are associated with skull length, the visceral and cerebral parts of the skull, and skull width and height at the base.

The peer-review process of our manuscript revealed a discrepancy in Kim et al. (2015), while Figure 2 illustrates a specific method for taking the LFB (Least frontal breadth), LBO (Greatest breadth across the orbits), and ZB (Zygomatic breadth) measurements, the actual measurements reported in the paper appear to have been obtained using a different technique. As our measurements strictly followed the protocol shown in their figure, a direct comparison with their published data was not feasible. These variables were therefore excluded from our statistical analysis, though the data are provided in Appendix B.

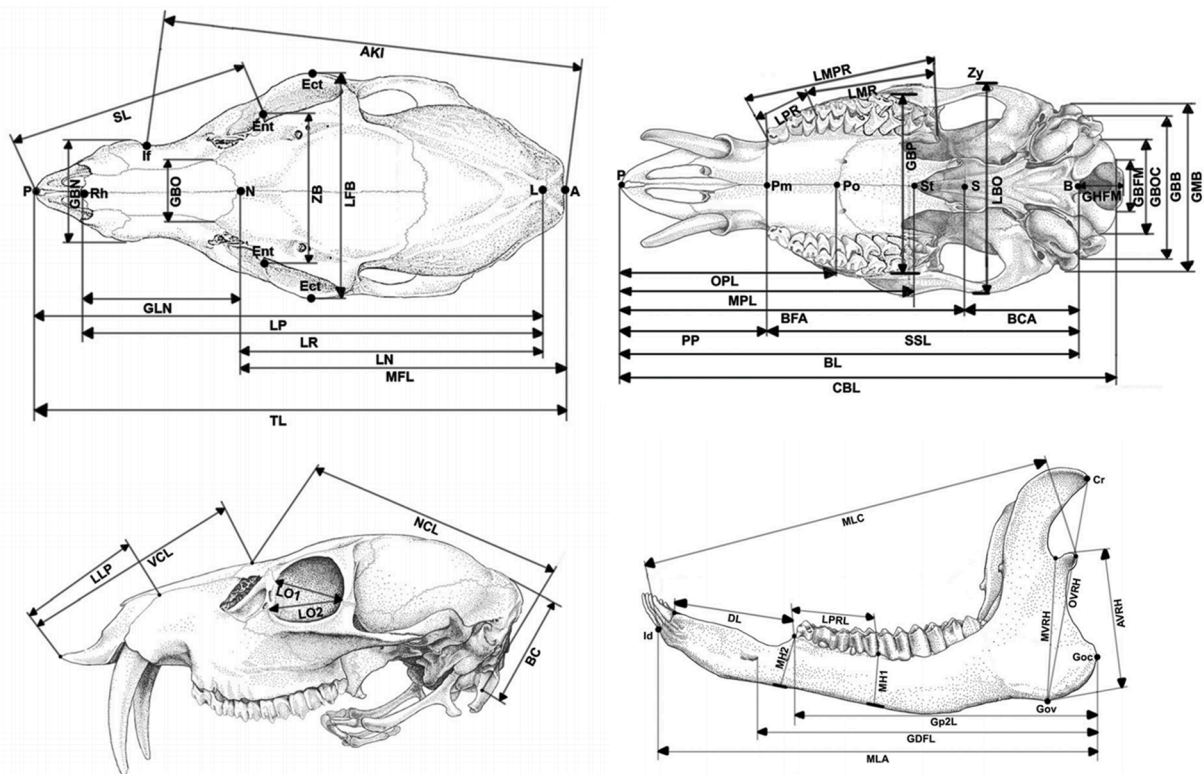


Figure 2. Scheme of skull measurements (after Kim et al. 2015) and mandible measurements of the water deer (after Kim et al. 2013); explanations of measurement abbreviations are provided in Appendix B.

Table 1. Craniometric characteristics of adult male water deer from Central China (according to Kim et al. 2015), South Korea (according to Kim et al. 2015, Kim et al. 2013), and the Russian Far East (our data). Bold values indicate statistically significant differences ($p < 0.05$).

Measurements	Central China (n = 30)		South Korea (n = 28)		Russian Far East (n = 8)			p value	
	Average (mm)	SD	Average (mm)	SD	Average (mm)	SD	Limits	Russian Far East vs. Central China	Russian Far East vs. South Korea
CRANIUM									
TL (Total length)	169.22	3.96	168.33	4.87	175	4.4	171-183	0.02405	0.01414
CBL (Condylobasal length)	158.59	3.67	158.24	5.19	164	4.3	160-172	0.02386	0.01913
BL (Basal length)	148.62	3.50	147.79	4.99	154	3.4	151-160	0.01279	0.007083
SSL (Short skull length)	94.29	2.43	94.36	2.34	98	2.5	96-103	0.003223	0.003554
PP (Premolare-Prosthion)	54.24	1.92	53.39	3.07	57	2.9	53-60	0.08211	0.03452
BCA (Basiscranial axis)	36.99	2.11	36.64	1.62	34	4.9	25-40	0.126	0.1691
BFA (Basifacial axis)	113.81	3.60	113.31	3.81	122	9.1	66-139	0.08845	0.07466
NCL (Neurocranium length)	93.78	3.41	93.21	3.33	94	3.2	65-99	0.9798	0.6517
VCL (Viscerocranium length)	81.29	3.06	81.26	3.56	86	3.7	50-89	0.03955	0.03864
MFL (Median frontal length)	94.54	3.20	93.80	3.23	95	2.3	91-98	0.8048	0.2837
LN (Lambda - Nasion)	83.32	3.35	83.25	3.09	84	3.5	77-88	0.7351	0.6944
LR (Lambda - Rhinion)	133.34	4.76	135.56	3.86	139	4.3	133-145	0.01337	0.07975
LP (Lambda - Prosthion)	160.73	4.31	160.67	4.80	169	6.6	163-178	0.02785	0.02716
GLN (Greatest length of the nasals)	50.93	3.93	52.91	3.50	55	3.8	49-61	0.02516	0.1673
SL (Snout length)	81.13	2.63	80.67	2.82	87	3.4	81-90	0.00695	0.005159
MPL (Median palatal length)	97.40	3.54	95.61	4.38	102	2.9	98-106	0.01639	0.003969
OPL (Oral palatal length)	73.20	2.31	72.40	3.46	76	3.9	72-83	0.1851	0.09754
LLP (Lateral length of the incisive bone)	46.69	3.00	46.72	3.06	48	3.9	44-54	0.5069	0.5176
LMPR (Length of the upper molar and premolar row)	48.84	1.96	50.17	2.22	52	2.1	47-53	0.01197	0.1046
LO1 (Length of the orbit - upper suture)	25.51	0.79	25.44	1.04	26	0.9	24-27	0.733	0.5857
LO2 (Length of the orbit - lower suture)	24.99	0.93	25.24	1.22	27	0.9	25-28	0.002446	0.006298
GMB (Greatest mastoid breadth)	47.39	1.93	47.28	1.62	52	1.8	45-55	0.000545	0.00048
GBOC (Greatest breadth of the occipital condyles)	28.21	1.21	29.21	2.41	29	1.8	26-31	0.1046	0.7994
GBB (Greatest breadth at the bases of the paraoccipital processes)	40.81	1.57	41.87	1.27	47	3.3	41-52	0.001919	0.005726
GBFM (Greatest breadth of the foramen magnum)	13.86	0.83	14.39	0.83	14	1.7	13-18	0.416	0.9806
GHFM (Greatest height of the foramen magnum)	14.64	0.94	14.87	0.82	16	2.0	13-19	0.2054	0.3201
BC (Basion - the highest point of the superior nuchal crest)	40.92	1.48	41.72	1.54	44	1.2	42-45	0.0002375	0.001697
MANDIBLE									
MLA (Mandible length from the angle)	-	-	136.42	-	140	5.4	131-146	-	0.1656
MLC (Mandible length from the condyle)	-	-	130.27	-	136	4.2	132-143	-	0.0222
Gp2L (Gonioncaudale - oral border of the alveolus of p2)	-	-	89.13	-	91	1.8	88-93	-	0.05869
GDFL (Gonioncaudale - the most aboral indentation of the dental foramen)	-	-	105.75	-	106	2.9	101-110	-	0.875
DL (Length of the diastema)	-	-	41.68	-	45	2.8	41-48	-	0.03478
AVRH (Aboral height of the vertical ramus)	-	-	40.77	-	40	2.2	36-43	-	0.6989
MVRH (Middle height of the vertical ramus)	-	-	38.75	-	39	1.6	37-42	-	0.4108
MH1 (Height of the mandible in front of m1)	-	-	14.33	-	15	1.0	13-16	-	0.537
MH2 (Height of the mandible in front of p2)	-	-	14.02	-	14	0.9	13-15	-	0.649

Dash - no data.

Kim Yun-Kun and colleagues (Kim et al. 2015) argued that there are no clear morphometric differences between water deer in South Korea and Central China. Although their univariate analysis suggested that *H. i. argyropus* is slightly larger than *H. i. inermis* in seven major cranial measurements, Student's *t*-test and principal component analysis showed that these two subspecies are poorly differentiated and share overlapping morphological traits.

A phylogenetic analysis of mtDNA revealed close genetic similarity between *H. i. inermis* and *H. i. argyropus*: the average genetic distance was 2.1% in the control region and 1.3% in cytochrome b (Koh et al. 2009). Two sympatric phylogroups (lineages A and B) were identified: only lineage A occurs in Central China, while both lineages A and B are present in South Korea

(Kim et al. 2014). A genetic study of water deer from the Tumen (Tumannaya) River area (three samples from Khasansky District, Russia, and two from Hunchun, China) revealed individuals from both lineages A and B (Li et al. 2022). The emerging trans-boundary population between Russia and China shows close phylogenetic affinity to the South Korean water deer (*H. i. argyropus*), but two of the four identified haplotypes were previously unrecorded and may belong to water deer from North Korea.

Historical distribution data—including archaeological and paleontological findings (Choe et al. 2020; Stimpson et al. 2021; Gao et al. 2023) and early descriptions (Swinhoe 1865, 1870; Brooke 1872; Swinhoe 1873; see also review in Ohtaishi and Gao

1990)—suggest that the species' range was once continuous. The observed genetic and morphological patterns indicate that isolation is likely too recent to have resulted in significant cranial or mtDNA differentiation.

Our data show that cranial differences between the newly formed Russian population and those of Central China and South Korea exceed the differences observed between the Chinese and Korean populations themselves.

Bergmann's rule states that body size negatively correlates with ambient temperature, particularly within species, and has been cited as a key factor shaping geographic variation in mammals (Bergmann 1847; Mayr 1956). The habitat of the Chinese water deer is located around 30° N latitude, and in South Korea, deer are found around 35–38° N. Yet skull sizes in these two populations do not differ substantially (Kim et al. 2015). The climate conditions in these regions are quite similar: the average annual air temperature is +16.6°C in Shanghai and +11.3°C in Seoul, with annual precipitation of 1327 mm and 1233 mm, respectively (Climate data... 2025).

In contrast, in the Russian Far East (data from the Tsukanovo Meteorological Station, Primorsky Krai), the climate is colder and drier: +5.7°C average annual temperature and 761 mm annual precipitation, with winter snow cover typically 5–10 cm deep. Under these harsher conditions (42–43° N), the deer are significantly larger.

It is also possible that the northward expansion is facilitated by more robust and larger individuals, especially considering that water deer must cross the Tumen River, which marks the border between North Korea, Russia, and China. While this hypothesis is plausible, it is not exhaustive. A more objective assessment of cranial metrics for this new population will require expanded sampling across all age and sex classes.

One of the defining features of the water deer is the presence of upper canine teeth, which occur in both males and females. In males, canines typically erupt at 6–7 months of age, reach about 50% of their final length the following spring, and attain full size by

Table 2. Skull measurements of adult male water deer (our data), musk deer (according to Prikhod'ko 2004), and Siberian roe deer (according to Danilkin 1999) (M±m, in mm).

Measurements	Musk deer <i>Moschus moschiferus turowi</i>	Water deer <i>Hydropotes inermis</i>	Siberian roe deer <i>Capreolus pygargus</i>
1. Total length	147.3±1.23	175.0±4.05	230.6±0.8
2. Condylobasal length	137.6±1.30	164.2±4.26	217.9±0.6
3. Basal length	128.1±1.34	153.8±3.37	204.0±0.7
4. Least frontal breadth	66.7±0.45	70.6±5.04	101.3±0.7
5. Interorbital width	37.3±0.33	37.6±1.93	62.5±0.6
6. Length of the visceral cranium	71.4±0.78	86.6±2.51	120.3±0.5
7. Greatest length of the nasals	52.4±0.70	55.1±3.76	75.7±0.8
8. Length of the upper tooth row	39.1±0.40	51.7±2.14	66.7±0.5
9. Greatest width of the cerebral cranium	45.6±0.20	49.3±1.98	65.6±0.4
10. Mandible length from the condyle	113.3±1.00	135.8±4.17	182.7±0.7
11. Length of the lower tooth row	42.2±0.78	57.2±3.76	73.4±0.5
12. Length of the diastema	35.6±0.50	45.0±2.83	52.9±0.7
13. Length of the canine	64	60 ^a	–

^a –Maximum length.

18–24 months (Cooke and Farrell 1998). The canines grow gradually in our sample; lengths ranged from 1.2 cm in juvenile males to 6 cm in adults (Figure 3). Interestingly, even during the early eruption stage in juveniles, the canine is already fully formed, with the visible tip representing only a small portion of its total length. The main portion lies within the alveolus, with the root positioned near the caudal edge of the nasal bones (Figure 3a, b). As the tooth grows, the root “descends,” and in adults, it often no longer reaches the level of the nasal bones (Figure 3d–f). Males frequently use canines for territorial defense and mating competition, which

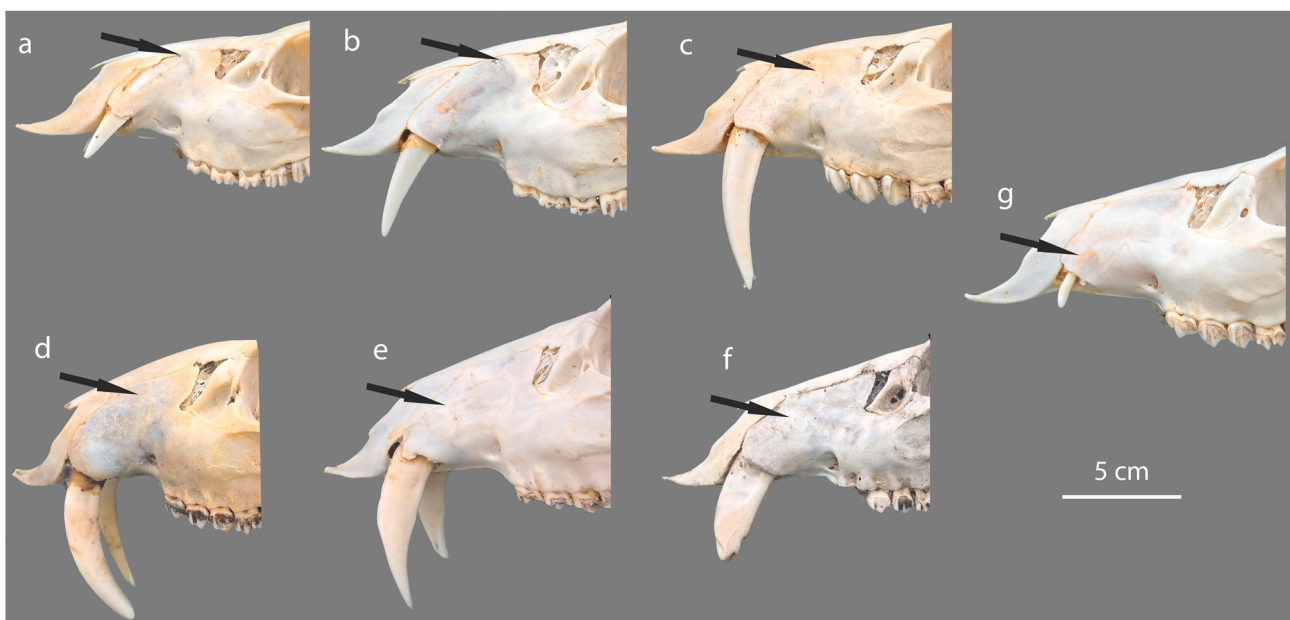


Figure 3. Stages of canine growth in the water deer. a–f (a – No. 14, age group II; b – No. 4, age group II; c – No. 9, age group III; d – No. 10, age group III; e – No. 5, age group IV; f – No. 16, age group III)—male canines at various stages of eruption; g (No. 7, age group III)—canine of an adult female. Arrows indicate the upper boundary of the canine root.

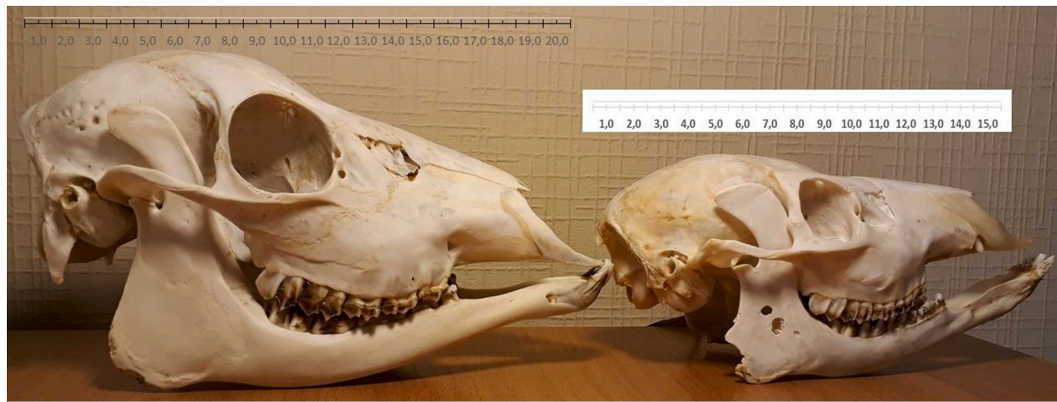


Figure 4. Skulls of adult female Siberian roe deer and water deer from the Khasansky District, Primorsky Krai, Russia.

often leads to breakage (Li et al. 2023). In our sample, four out of eight adult males had broken canines, and one showed unusual anterior wear (Figure 3e).

The canines of females are small, not exceeding 1 cm in length, and do not protrude from the mouth (Figure 3g). However, the most important difference between the canines of female and male water deer is not their length—since in males the canines may be broken or only beginning to erupt—but their basal width. In males, the canines are wide, with a basal width of 5–14 mm and a massive root; in females, the canines are thin, never exceeding 3 mm at the base, with a short, slender root.

Sexual dimorphism in water deer is pronounced not only in canine size. Unlike most cervids, female skulls are larger than those of males, although this is not always evident in mandibular measurements (Kim et al. 2013). Our collection includes only three female skulls of different ages, which does not allow us to assess age-related variation based on our material.

Water deer are significantly smaller than the Siberian roe deer *Capreolus pygargus* (Pallas, 1771), but larger than the musk deer. According to our sample, the average body mass of water deer in the southern Russian Far East is 19.2 kg (ranging from 18.0 to 19.8 kg) (Darman et al. 2022), while roe deer from the same region weigh approximately twice as much—between 34.3–39.2 kg (Bromlei and Kucherenko 1983). In contrast, the adult Far Eastern musk deer (*Moschus moschiferus turowi* Zalkin, 1945) weighs between 7.1 and 11.8 kg (Prikhodko 2003).

In terms of craniometric characteristics, the water deer is also significantly smaller than the Siberian roe deer in the southern Russian Far East (only males were compared), with skull measurements being 35–40% larger in roe deer (Table 2, Figure 4). Meanwhile, most cranial parameters in water deer are, on average, 20% larger than those of the Far Eastern musk deer, except for skull width, which differs by only 5–8% (Table 2).

Conclusion

In this study, 50 cranial measurements were taken from 15 skulls of water deer from the Russian Far East. A comparative cranial analysis with samples from Central China and Korea revealed that water deer from Russia are significantly larger in 16 cranial measurements. These morphometric parameters can be used in the field for identifying skulls and their fragments, as well as for recognizing fossilized bone remains.

The obtained cranial characteristics clearly distinguish water deer from both the Siberian roe deer and the Far Eastern musk deer.

When determining the sex of water deer based on canines, it is important to consider not only their length—since in males the canines may be broken or only beginning to erupt—but also the basal width. In males, the basal width of the canine ranges from 5 to 14 mm depending on age, while in females it does not exceed 3 mm.

Further accumulation of data on water deer from the southern Russian Far East will enable more detailed studies of cranial differences between sexes and age-related morphological changes.

CRedit authorship contribution statement

Valeriya Omelko: Writing – review & editing, Writing – original draft, Methodology. **Yury Darman:** Writing – review & editing, Data curation, Conceptualization. **Gleb Sedash:** Writing – review & editing, Data curation.

Declaration of competing interest

V The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.japb.2026.02.006>.

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