



Short communication

Cranial suture closure pattern in water deer and implications of suture evolution in cervids

Jinwoo Oh^a, Yung Kun Kim^b, Masahiro Yasuda^c, Daisuke Koyabu^{d,*}, Junpei Kimura^{a,**}

^a Department of Anatomy and Cell Biology, College of Veterinary Medicine, Seoul National University, Seoul, Republic of Korea

^b Bureau of Ecological Research Division of Basic Research, National Institute of Ecology, Seocheon-gun, Chungcheongnam-do, Republic of Korea

^c Veterinary Anatomy, University of Miyazaki, Miyazaki, Japan

^d The University Museum, The University of Tokyo, Tokyo, Japan

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ABSTRACT

Interspecific diversity exists in cranial suture closure patterns among mammalian species. Suture closure patterns partly reflect phylogenesis, but it has also been claimed that it is influenced by biomechanical factors. Here we provide the first report on the cranial suture closure pattern in water deer. Among cervids, the water deer is an exceptional species, as it is the only one without antlers. Instead, the male water deer possess prominent canines, which are utilized during male–male combats. This unique morphological setting allowed us to examine whether the presence of prominent canines affects cranial suture closure. We found that the only sexual difference in cranial suture closure pattern is the closure of the interfrontal suture in males, which is found in some other cervid species as well. Except for the interfrontal suture closure, timing and sequence of cranial suture closure were comparable between both sexes, suggesting that the presence of prominent canines in males has no influence on cranial suture closure pattern. Our results indicate that interfrontal suture closure in males is a phylogenetic pattern, *i.e.* an apomorphy for Capreolini, Hydropotini and Alceini.

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Cranial suture, a fibrous tissue uniting the bones of the skull, comprises rapidly dividing mesenchymal progenitor cells, and in general, cranial sutures remain open during skull growth and tend to close with arrested growth (Opperman, 2000; Richtsmeier and Flaherty, 2013). The sequence of cranial suture closure of mammals follows a general pattern, *i.e.* vault, basilar, circummeatal, palatal, facial, and then craniofacial (Krogman, 1930). In most mammals the sutures around the foramen magnum and cranial base generally close earlier than other sutures (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014; Sánchez-Villagra, 2010). Many variations among mammalian species are also known. Ruminants show fewer closed sutures than other artiodactyls (Bärmann and Sánchez-Villagra, 2012), and placental mammals show more closed sutures than marsupials (Rager et al., 2014). In primates, the suture closure pattern of the cranial vault is reported to clearly reflect

the phylogenetic history (Cray et al., 2014). These growing evidences suggest that sequence variations largely reflect phylogeny, but the interspecific difference in cranial suture pattern itself is argued to be affected by biomechanical factors, such as brain expansion (Henderson et al., 2004) and masticatory forces (Sun et al., 2004). In particular, physical dynamics are known to affect the fusion or non-fusion of sutures (Moazen et al., 2009). Sutures can be different, depending on the direction of the forces that sutures experience (Wang et al., 2012). Tensile stress promotes bone deposition in the suture, whereas compressive stress prevents bone deposition (Wagemans et al., 1988). Thus, a suture that experiences considerable tension tends to be closed, whereas a suture under compression tends to remain open. For example, in *Pecari tajacu*, where the palatal sutures close extremely early, biomechanical requirements related to the feeding mode may affect this unusual suture closure pattern (Bärmann and Sánchez-Villagra, 2012).

The water deer (*Hydropotes inermis*) is a cervid species native to China and Korea. Two subspecies are distinguished: *H. i. inermis* from the Yangtze River basin in China and *H. i. argyropus* from Korea (Geist, 1998). Water deers inhabit areas near water with tall grasses (Cooke and Farrell, 1998). England and France also harbor introduced populations (Cooke and Farrell, 1998; Dubost et al., 2008). Although the overall growth pattern of the skull is similar between

* Corresponding author at: The University Museum, The University of Tokyo, 7-3-1 Hongo, Tokyo, 113-0033, Japan.

** Corresponding author at: Department of Anatomy and Cell Biology, College of Veterinary Medicine, Seoul National University, Seoul, 151-742, Republic of Korea.

E-mail addresses: jw106@snu.ac.kr

(J. Oh), isys1215@gmail.com (Y.K. Kim), yasudaja@cc.miyazaki-u.ac.jp (M. Yasuda), koyabu@um.u-tokyo.ac.jp (D. Koyabu), kimura@snu.ac.kr (J. Kimura).

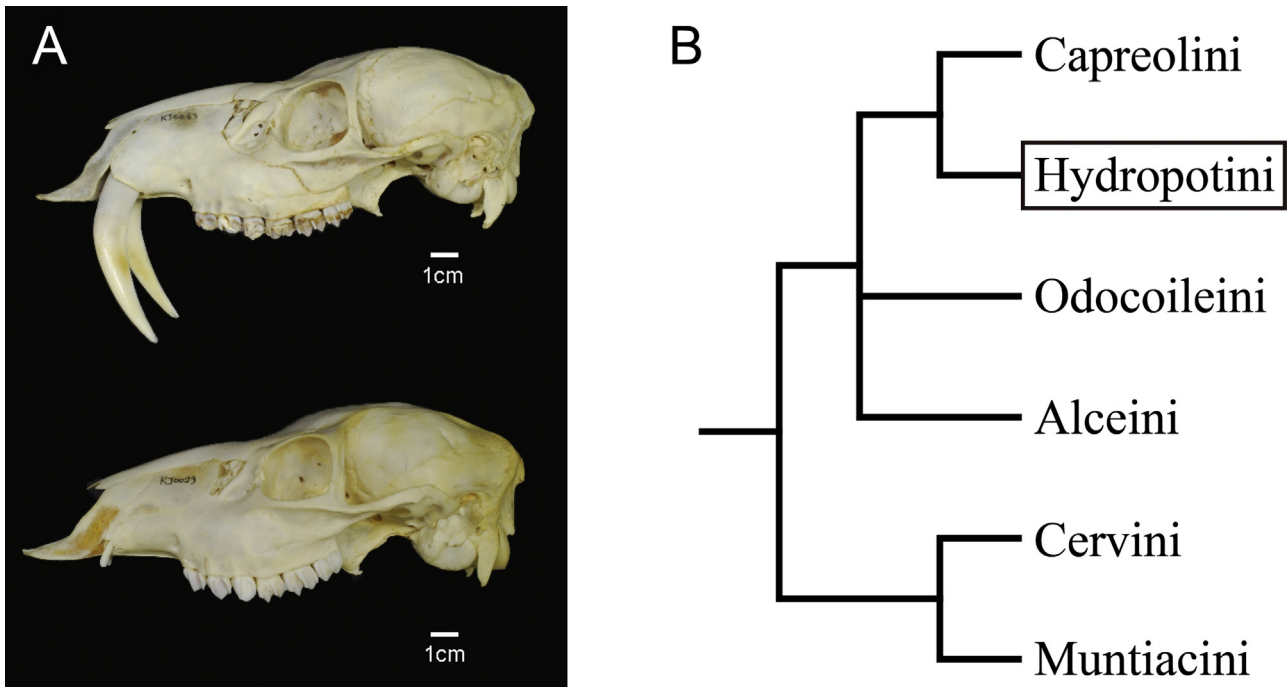


Fig. 1. (A) Upper: skull of male water deer; Lower: skull of female water deer. Canines are largely developed only in males. Both sexes do not possess antlers. (B) Phylogenetic tree of tribes in Cervidae based on study of Gilbert et al. (2006).

the sexes (Kim et al., 2013b), female water deer have a slightly larger skull than males (Kim et al., 2013a). It is reported that the layers of masseter muscle in water deer are rather simplified compared with that in other cervids (Sasaki et al., 2013). It is a unique species as it is the only cervid species that completely lacks antlers but possesses sabre-like canines (Fig. 1A).

Pronounced sexual dimorphism is seen in the canines as they are well developed in males but very short in females. During combat, male water deer strike opposing males with their heads to inflict damage with their large canines (Aitchison, 1946; Cooke and Farrell, 1998). Male mouse deer and musk deer are similar to water deer as they also lack antlers and instead possess prominent canines; however, unlike water deer they do not belong to the Cervidae. All recent phylogenetic studies agree that Tragulidae (mouse deer) is the sister taxon of all other ruminants (Agnarsson and May-Collado, 2008; Fernández and Vrba, 2005; Hassanin and Douzery, 2003; Wallis and Wallis, 2001). Moschidae (musk deer) is the sister group of either Cervidae (Fernández and Vrba, 2005) or Bovidae (Hassanin and Douzery, 2003).

Because of the supposedly primitive morphological characters, i.e., large canines and absence of antlers, water deer was once thought to be the most basal cervid taxon (Lister, 1984). However, recent genetic analyses and studies on other morphological traits suggest that the phylogenetic position of water deer is within other antlered cervids and especially close with the genus *Capreolus* (Pitra et al., 2004; Randi et al., 1998; Gilbert et al., 2006) (Fig. 1B). Given the phylogenetic position of the water deer and the presence of antlers in other deer species, it is now widely believed that the antlers were secondarily lost in this species.

Here we describe the cranial suture closure pattern of water deer. We examined the effect of large canines in male water deer, which are routinely employed during male–male combat, on suture closure pattern. 20 male and 15 female water deer skulls were analyzed. All specimens were collected from the wild in Korea (*H. i. argyropus*) and stored at the College of Veterinary Medicine, Seoul National University (Seoul, South Korea). Data from the specimens are summarized in Appendix A.

The suture closure level was measured for 29 cranial sutures: interincisive, incisive-maxillary, internasal, nasal-maxillary, intermaxillary, maxillary-lacrimal, maxillary-palatine, maxillary-zygomatic, interpalatine, lacrimal-zygomatic, nasal-frontal, lacrimal-frontal, zygomatic-frontal, zygomatic-temporal, presphenoid-frontal, presphenoid-basisphenoid, presphenoid-palatine, basisphenoid-parietal, basisphenoid-temporal, basisphenoid-basioccipital, interparietal, frontal-parietal, interparietal, parietal-temporal, parietal-supraoccipital, temporal-supraoccipital, temporal-exoccipital, supraoccipital-exoccipital, and exoccipital-basioccipital.

Closure levels of observed cranial sutures were scored as 0, not fused; 1, $\frac{1}{4}$ fused; 2, $\frac{1}{2}$ fused; 3, $\frac{3}{4}$ fused; and 4, totally fused. This scoring is modified from what was used by Wilson and Sánchez-Villagra (2009). Closure sequence was determined by the number of specimens showing closed sutures. Sutures are ranked as earlier closing suture when they are closed in more specimens. Closure levels 3 and 4 are considered closed sutures as in other studies (Rager et al., 2014; Wilson and Sánchez-Villagra, 2009). The sums of all closure level scores of each specimen is used to evaluate its overall closure level. A Kendall's tau-b correlation between the male and female water deer suture closure sequences was calculated to assess correspondence between the two sequences, as in Wilson and Sánchez-Villagra (2009). Kendall's tau-b measures cross-tabulation associations between two rankings. The rank in each sex was created to represent the order of suture closure following Wilson and Sánchez-Villagra (2009). The test was performed using SPSS version 21.0 statistical software.

Unfortunately a precise age determination of wild-caught water deer is impossible. However, it is known that after maturation the height of the cheek teeth and especially the first lower molar (M_1) generally decreases with age in cervids (Ozaki et al., 2010). M_1 quickly erupts after birth in the water deer, and M_1 height decreases with growth (Kim et al. 2013b). All specimens in this study exhibited fully erupted M_1 . Therefore, we treated M_1 height as a proxy for age. As was done in Bärmann and Sánchez-Villagra (2012), individuals with very advanced tooth wear were treated as cases showing

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