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Analysis of Cranial Suture Closure Pattern and Development of Non-invasive Age Estimation Method in Cervids

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Analysis of Cranial Suture Closure pattern and Development of Non-invasive Age Estimation Method in Cervids

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ABSTRACT

The cranial suture is fibrous tissue at the junction of bones which consists of the skull. Suture allows bone deposition at the margin of cranial bones in young individuals. Eventually, sutures are ossified and disappear in mature individuals. Closure timings are different in each suture and make the unique pattern of closure

which is different among many mammal species. Comparative studies on cranial suture closure can provide helpful information because the closure pattern reflects growth, behavior and evolutionary patterns of mammals. In this study, cranial suture closure patterns of three cervid species in Northeast Asia are observed and insights to its implications in Cervidae species will be provided.

In chapter I, cranial suture closure pattern of the Korean water deer (*Hydropotes inermis*) was observed. Among cervids, water deer is an exceptional species as it is the only cervid which lost its antlers. In contrast to other cervid males, males of water deer possess prominent canines, which are utilized during male-male combats. This unique morphological setting in water deer allowed us to test whether the presence of prominent canines affects cranial suture closure. It was found that the sequence of cranial suture closure was little related to canine teeth. Canine teeth of water deer are embedded in soft tissue at alveoli which is larger than its teeth, and this structure decreases the physical impact. Unique behavior pattern does not always influence closure pattern of cranial suture even though it is expected to have a huge physical impact.

In chapter II, cranial suture closure patterns of Siberian roe deer (*Capreolus pygargus*) in Jeju Island and Japanese sika deer (*Cervus nippon*) were observed and

patterns of eleven species of cervids were compared. Patterns like variation rate and number of closing sutures distinguished species and clades from others. Timing of the interparietal suture closure was highly variable within *Capreolus pygargus*. Cranial suture closure pattern of European roe deer (*Capreolus capreolus*) similarly showed intraspecific variation of the interparietal suture closure, whereas other cervid species studied to date did not show any intraspecific variation in the sequence of cranial suture closure. Such high intraspecific variation of the interparietal suture closure may be a derived character for *Capreolus*. Other cervid species except *Cervus nippon* in tribe Cervini showed additional closure of cranial sutures more than five sutures which commonly closed in all Cervidae species. *Cervus nippon* did not show additional full closures of cranial sutures, however, showed partial closures of several cranial sutures which closed in other species of tribe Cervini. *Cervus nippon* might evolved to reduce closure of cranial sutures.

In chapter III, relationship between cranial suture closure pattern of sika deer in Kinkasan Island of Japan and age was assessed. Interparietal and exoccipital-basioccipital sutures closed in fawns, supraoccipital-exoccipital and basisphenoid-basioccipital sutures closed in young adults, and presphenoid-basisphenoid sutures

closed in adults. A strong positive relationship between the sum of suture closure level scores and age was found. It was found that this relationship was even stronger than the relationship between age and the crown height of the first molar, which is frequently used for non-destructive age determination. These results suggested that age at death of sika deer can be estimated using closure pattern of cranial sutures by the formula $Age = 0.8296 \times (Sum\ of\ closure\ level\ scores) - 4.8482$ for male sika deer, and $Age = 0.8892 \times (Sum\ of\ closure\ level\ scores) - 5.5923$ for female sika deer. Age estimation by cranial suture showed high reliability considering that ages of 82 specimens among totally 87 specimens which used in this study are predicted within 95% confidence interval of the formula. Age estimation by cranial suture is advantageous compared to other non-invasive age estimation methods because it can be applied to both sexes and specimens with old ages. This study highlights the potential of cranial suture closure pattern as an alternative non-invasive approach for age estimation.

Skull is very important specimen frequently used in morphological study of mammals because ecological and phylogenetical features are reflected in it. This makes understanding of skull important. Understanding of cranial suture which is

important structure of skull will be helpful in studies about phylogenetic relationship and ecological features of mammal species. Age is also very significant information in study of mammals. It is essential information in study of growth and reproductive patterns. Accurate age estimation with more indicators will contribute to many studies. Understanding of cranial suture and age estimation by it will provide important information to research. In conclusion, cranial suture closure pattern in cervids is highly related with age, and variations of patterns among species are influenced by phylogenetic relationship rather than physical stress or morphological features. Age of cervids can be estimated by cranial suture closure pattern avoiding destruction of specimen. Results of this study will contribute to researches on cervids in future.

KEY WORDS: Cranial suture, Siberian roe deer, Sika deer, Skull, Water deer

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GENERAL INTRODUCTION

General Characteristics of Cranial Suture

Skull is the bone which exists in animals of Craniata including mammals. It supports and protects brain and facial structures. Skull consists of many bony parts, and adjacent bony parts make the junction between them. Cranial suture is a fibrous tissue at the junction comprises rapidly dividing mesenchymal progenitor cells (Opperman, 2000; Richtsmeier and Flaherty, 2013). In general, cranial sutures remain open during skull growth and allow bone deposition at sutural margin. Eventually, cranial sutures close and its line disappears when growth of surrounding bones is completed (Opperman, 2000; Richtsmeier and Flaherty, 2013).

Timing of suture closure within the individual is different among each cranial suture (Todd and Lyon, 1924). The 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 pattern of sutures around the foramen magnum and cranial base generally fuses earlier than other sutures

(Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014; Sánchez-Villagra, 2010). Many variations among mammalian species are also known. Pattern of cranial suture closure is studied by many researchers to find out characteristics and academic usefulness of cranial suture.

Relationship between Cranial Suture and Biomechanical Stress

Several studies noted the relationship between biomechanical stress and cranial suture. Closure of cranial suture is influenced by direction of mechanical forces that suture experience (Wang et al., 2012). Tensile stress promotes bone deposition in the suture, whereas compressive stress prohibits 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. These characteristics of cranial suture might be related to adaptation to mechanical stress.

Henderson et al. (2004) found that both sutural strain by pressure resulted from intracranial expansion and bone deposition rate at suture site decrease with age. It means that mechanical stress influences bone deposition at suture. However, mechanical strain itself was too small to influence osteoblast activity at suture site. Influence of unknown mechanism which transduces or magnifies biomechanical signal by sutural strain to osteoblast activity was expected.

Sun et al. (2004) studied about relationship between masticatory forces and suture closure in pig. Posterior interfrontal suture and anterior interparietal suture are influenced by masticatory forces. Polarity of strain was always tensile in

interparietal suture and changed from pure compressive to both compressive and tensile in interfrontal suture with increasing age. Interparietal suture showed closure in some pigs, but it closed from ectocranial side not like usually known suture closure. Thickening of bone is the expected reason of this unusual closure. Thickness of bone might have obstructed diffusion of osteoinbihitory signal from dura mater. It is also conceivable that periosteum correlated to bone thickening induced suture fusion directly.

Moazen et al. (2009) used computer modelling of lizard skull to assess role of cranial suture. Computer modelling of *Uromastys hardwickii* was constructed based on micro-computed tomography data and finite element analysis was performed on modelling. Skull modelling with no sutures showed high stress pattern on region which normally cranial suture is located. Skull modelling with sutures showed relieved stress pattern on same region. These findings provide an insight to function of cranial sutures.

In species that have unique behaviors, additional factors may influence cranial suture. Among artiodactyl species which Bärmann and Sánchez-Villagra (2012) described, *Pecari tajacu* showed unique pattern of cranial suture closure. Palatine sutures of *Pecari tajacu* showed close extremely early closure compared to other

adjacent species. Biomechanical requirements related to the feeding mode may affect this unusual suture closure pattern. This species uses its snout for rooting and high mechanical stress is expected around the palate.

Phylogenetic Implication of Cranial Suture

Many researches are trying to find phylogenetic meaning among variations of cranial suture closure pattern in mammals. It has been known that closure timing of cranial sutures is often different between taxonomic groups. Many evidences suggest that variations of suture closure patterns strongly reflect phylogenetic history.

Wilson and Sánchez-Villagra (2009) observed cranial suture closure pattern of hystricognath rodents. Pattern is conserved in whole hystricognath group and more conserved in selected clades. Cranial sutures contacting exoccipital, interparietal and palatine bones showed early closure. Sutures contacting exoccipital bone showed the highest level of full closure across all species.

Bärmann and Sánchez-Villagra (2012) observed cranial suture closure pattern of many terrestrial artiodactyl species. Ruminants showed fewer closure of sutures than non-rumanint species. Body mass and closure rates of cranial sutures showed positive relationship. All species showed early closure of cranial sutures surrounding foramen magnum. Giraffid species showed early closure of supraoccipital-parietal suture.

Pattrns of cranial suture closure in carnivoran species are studied by Goswami et al. (2013). High variability of palatine suture closure in carnivoran species is distinguished from other mammalian clades. Size and cranial suture closure level did not have correlation in carnivoran species. Phylogenetic signal from cranial suture closure pattern was only found in musteloid species.

Cranial suture closure patterns of many mammalian species including marsupials are observed by Rager et al. (2014). Closure level of cranial sutures did not have significant correlation with body mass. It was high in Afrotheria and Xenarthra. Basisphenoid-basioccipital and exoccipital-basioccipital sutures close in all species. Supraoccipital-exoccipital and interparietal sutures close in most species. Intraspecific variation of suture closure pattern was high in Xenarthra and low in Afrotheria. Placental mammals show more closed sutures than marsupials.

Age Determination by Cranial Suture Closure Pattern

Generally, cranial sutures are opened in immature individuals, and disappear in old individuals when growth of surrounding cranial bones is completed (Opperman, 2000; Richtsmeier and Flaherty, 2013; Todd and Lyon, 1924). Accordingly, the degree of suture closure is highly correlated with age. Pattern of cranial suture closure has potential to become a useful tool in age determination.

In humans, cranial suture closure has already been often used to estimate age in forensic and archaeological area (Key et al., 1994; Meindl and Lovejoy, 1985).

Todd and Lyon (1924) observed skull specimens of male humans and described relationship between age and suture closure. Cranial sutures at vault region started closure around middle of twenties and completed closure around late thirties or early forties. Cranial suture around circum meatal region completed closure around seventies or eighties.

Meindl and Lovejoy (1985) observed cranial sutures of human skull specimens and compared lateral-anterior sutures with vault sutures and ectocranial sutures with endocranial sutures. For estimating old ages, lateral-anterior sutures were better than vault sutures and ectocranial sutures were better than endocranial

sutures.

Key et al. (1994) compared age estimation methods by endocranial sutures and ectocranial sutures. Endocranial sutures distinguished young and middle aged individuals but gave no information over age of fifty years. Ectocranial sutures predicted ages over fifties, however subjected to factors like sexual dimorphism and regional difference more than endocranial sutures. Estimation method was improved by several changes like more simple scoring and selection of sutures which more correlated with age.

Purpose of This Thesis

In this dissertation, there are three major topics. First, influence of physical stress to cranial suture closure pattern will be assessed using water deer which only male individuals show unique fight behavior. Second, phylogenetic implication of cranial suture closure pattern will be assessed among extant Cervidae species. Third, validity of age determination using cranial suture closure pattern will be assessed using sika deer specimens which have records of exact age. Through findings of three chapters, this study will confirm reflection of physical stress, phylogenetic relationship and growth on cranial suture closure pattern of cervids.

CHAPTER I

Cranial Suture Closure Pattern in Water Deer and Implications of Suture Evolution in Cervids

INTRODUCTION

The water deer (*Hydropotes inermis*) is a cervid species native to China and is found along the Yangtze River (*Hydropotes inermis inermis*) as well as in Korea (*Hydropotes inermis argyropus*) (Geist, 1998). Originally, it was distributed in areas near water with tall grasses (Cooke and Farrell, 1998). England and France also have introduced populations (Cooke and Farrell, 1998; Dubost et al., 2008). Although the overall growth pattern of the skull is similar between 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. 1).

Fig. 1. Left lateral view of water deer skulls. Upper: skull of male water deer, Lower: skull of female water deer.

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).

In this study, the cranial suture closure pattern of water deer was described for the first time. The effect of large canines was also examined in male water deer, which are routinely employed during male–male combat, on suture closure pattern.

MATERIALS AND METHODS

Skull of twenty male and fifteen female water deer were observed. All specimens were collected from the wild and stored at the College of Veterinary Medicine, Seoul National University (Seoul, South Korea). Data from the specimens are summarized in Table 1.

Table 1. Closure levels observed in cranial sutures of water deer specimens

Specimen Number	Sex	Interparietal	Exoccipital-Basioccipital	Supraoccipital-Exoccipital	Basisphenoid-Basioccipital	Presphenoid-Basisphenoid	Maxillary-Palatine	Parietal-Supraoccipital	Interfrontal	Interincisive	Incisive-Maxillary	Internasal	Nasal-Maxillary	Intermaxillary	Maxillary-Lacrimal	Maxillary-Zygomatic	Interpalatine	Lacrimal-Zygomatic	Nasal-Frontal	Lacrimal-Frontal	Zygomatic-Frontal	Zygomatic-Temporal	Orbitosphenoid-Frontal	Orbitosphenoid-Palatine	Alisphenoid-Parietal	Alisphenoid-Temporal	Frontal-Parietal	Parietal-Temporal	Temporal-Supraoccipital	Temporal-Exoccipital	Sum of Closure Level Scores	M_1 Height(mm)	Total Length(mm)
KJ0009	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	6.61	171.84
KJ0011	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	6.62	173.58
KJ0020	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	5.74	168.08
KJ0021	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	5.01	173.51
KJ0023	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	-	170.96
KJ0055	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	3.39	170.67
KJ0056	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	7.07	160.09
KJ0058	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	3.22	179.39
KJ0059	F	4	4	4	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	7.86	160.63
KJ0061	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	6.97	155.39
KJ0063	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	5.92	170.07
KJ0064	M	4	4	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	7.76	159.17

Table 1. continued

KJ0065	F	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	7.19	143.00
KJ0067	F	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	8.05	146.75
KJ0068	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	6.17	168.33
KJ0069	F	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	8.16	151.79
KJ0070	F	4	4	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	7.09	157.66
KJ0071	F	4	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	7.11	155.07
KJ0072	F	4	4	4	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	8.26	151.82
KJ0073	M	4	4	3	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	6.22	166.89
KJ0074	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	7.86	155.21
KJ0076	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	3.06	177.75
KJ0078	F	4	4	4	4	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	-	174.99
KJ0080	M	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	-	139.38
KJ0083	M	4	4	3	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	7.00	156.13
KJ0085	M	4	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	6.72	161.46
KJ0086	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	5.55	164.09
KJ0087	M	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	3.99	175.16
KJ0089	M	4	4	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	6.38	159.47
KJ0108	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	5.52	165.26
KJ0110	M	4	4	4	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	5.36	177.31
KJ0111	M	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	7.72	153.31
KJ0112	M	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	8.13	150.06

Table 1. continued

KJ0114	M	4	4	4	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	5.59	166.64
KJ0117	M	4	4	4	4	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	5.40	177.25

M=Male, F=Female; M_1=First lower molar; Closure level score : 0 (not fused), 1 (¼ fused), 2 (½ fused), 3 (¾ fused), and 4 (totally fused).

The suture closure level was measured in 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, orbitosphenoid-frontal, presphenoid-basisphenoid, orbitosphenoid-palatine, alisphenoid-parietal, alisphenoid-temporal, basisphenoid-basioccipital, interfrontal, frontal-parietal, interparietal, parietal-temporal, parietal-supraoccipital, temporal-supraoccipital, temporal-exoccipital, supraoccipital-exoccipital, and exoccipital-basioccipital.

Closure levels observed in cranial sutures were scored as 0, not fused; 1, ¼ fused; 2, ½ fused; 3, ¾ fused; and 4, totally fused. This scoring is modified from which used by Wilson and Sánchez-Villagra (2009). Closure sequence was determined by the number of specimens showing closed sutures (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014). Earlier closing sutures are closed in both young and old aged specimens. Later closing sutures are closed in old aged specimens but not in young aged specimens. So earlier closing sutures close in more specimens compared to later closing sutures do. Therefore, 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). Sums of closure level scores of each specimen were calculated by totalization of closure level score to evaluate overall closure level of specimen. Kendall's tau-b correlation was calculated between the male and female water deer suture closure sequences to assess correspondence between two sequences. The test was performed using SPSS version 21.0 statistical software.

Unfortunately there is still lack of detailed knowledge on age determination of the water deer. However, it is known that after maturation M_1 height generally decreases with age in cervids (Ozaki et al., 2010). As was done in Bärmann and Sánchez-Villagra (2012), individuals with very advanced tooth wear were treated as cases showing maximum possible suture closure. In this study KJ0055, whose closure score was highest but M_1 was shorter than one half of the individual with the tallest M_1, was regarded as the oldest individual with maximum possible suture closure among females (Table 1). With the same manner, KJ0087 was regarded as fully mature individual and the oldest individual among males.

Height of M_1 was measured from the cervical line on lingual side to the tip of metaconid by vernier calipers (Ozaki et al., 2010). Total length of the skull (Von den Driesch, 1976) was also recorded as an additional proxy of age. The relationship between the sum of closure level scores and M_1 height was examined

by linear regression in male and female respectively using PAST version 2.17c statistical software (Hammer et al., 2001) to evaluate correlation between overall closure level and age. The slopes of linear regression in male and female were compared to test the differences between both sexes. Two female and one male specimens which lack mandibles were excluded from this comparison because there is no data of M_1 height.

RESULTS

Documentation of the presence or absence of suture closure, closure level scores, M_1 height, and total skull length are given in Table 1. Acquired closure sequence of cranial sutures is described in Table 2. The interparietal and exoccipital-basioccipital sutures are the earliest closing suture in both sexes. Supraoccipital-exoccipital suture closes after interparietal and exoccipital-basioccipital suture closure, and it is followed by closure of basisphenoid-basioccipital suture. After these closures, presphenoid-basisphenoid suture closes in female. However, in male, interfrontal suture also closes with presphenoid-basisphenoid suture. No females showed closure of interfrontal suture. Maxillary-palatine and parietal-supraoccipital suture partially close. Other sutures, interincisive, incisive-maxillary, internasal, nasal-maxillary, intermaxillary, maxillary-lacrimal, maxillary-zygomatic, interpalatine, lacrimal-zygomatic, nasal-frontal, lacrimal-frontal, zygomatic-frontal, zygomatic-temporal, orbitosphenoid-frontal, orbitosphenoid-palatine, alisphenoid-parietal, alisphenoid-temporal, frontal-parietal, parietal-temporal, temporal-supraoccipital and temporal-exoccipital, remain open. No closed cranial sutures were found around the rostrum.

Table 2. Cranial suture closure sequences of water deer

Rank	Male	Female
1	Interparietal Exoccipital-Basioccipital	Interparietal Exoccipital-Basioccipital
2	Supraoccipital-Exoccipital	Supraoccipital-Exoccipital
3	Basisphenoid-Basioccipital	Basisphenoid-Basioccipital
4	Presphenoid-Basisphenoid Interfrontal	Presphenoid-Basisphenoid
Not closed	Interincisive Incisive-Maxillary Internasal Nasal-Maxillary Intermaxillary Maxillary-Lacrimal Maxillary-Palatine Maxillary-Zygomatic Interpalatine Lacrimal-Zygomatic Nasal-Frontal Lacrimal-Frontal Zygomatic-Frontal Zygomatic-Temporal Orbitosphenoid-Frontal Orbitosphenoid-Palatine Alisphenoid-Parietal Alisphenoid-Temporal Frontal-Parietal Parietal-Temporal Parietal-Supraoccipital Temporal-Supraoccipital Temporal-Exoccipital	Interincisive Incisive-Maxillary Internasal Nasal-Maxillary Intermaxillary Maxillary-Lacrimal Maxillary-Palatine Maxillary-Zygomatic Interpalatine Lacrimal-Zygomatic Nasal-Frontal Lacrimal-Frontal Zygomatic-Frontal Zygomatic-Temporal Orbitosphenoid-Frontal Orbitosphenoid-Palatine Alisphenoid-Parietal Alisphenoid-Temporal Interfrontal Frontal-Parietal Parietal-Temporal Parietal-Supraoccipital Temporal-Supraoccipital Temporal-Exoccipital

Interparietal suture and sutures around the foramen magnum close earlier than other sutures in both sexes, which is consistent with the general pattern found in many artiodactyl species (Bärmann and Sánchez-Villagra, 2012). The interfrontal suture of the cranium closes only in males, but it is unlikely to be related to the presence of prominent canines. Among ruminants, it is reported that in some species with elongated canines (e.g., *Tragulus javanicus* and *Hyemoschus aquaticus*) the interfrontal suture closes in mature individuals (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014). However, this is not the case for other species with elongated canines, such as *Moschiola meminna*, *Moschus moschiferus*, and *Muntiacus muntjak* (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014).

Kendall's tau-b coefficient between the sexes was 0.92 ($P < 0.001$), indicating that the cranial suture closure patterns are highly similar between the sexes. Fig. 2 illustrates the relationship between the M_1 height of the mandible and the sum of closure level scores for both sexes. The sum of closure level score increased with decrease of M_1 height. The 95% confidence interval for the slope of linear regression between the M_1 height and the sum of closure level score ranged from -2.274 to 0.07835 for males and from -2.413 to -0.4399 for females, indicating statistically no significant difference between sexes.

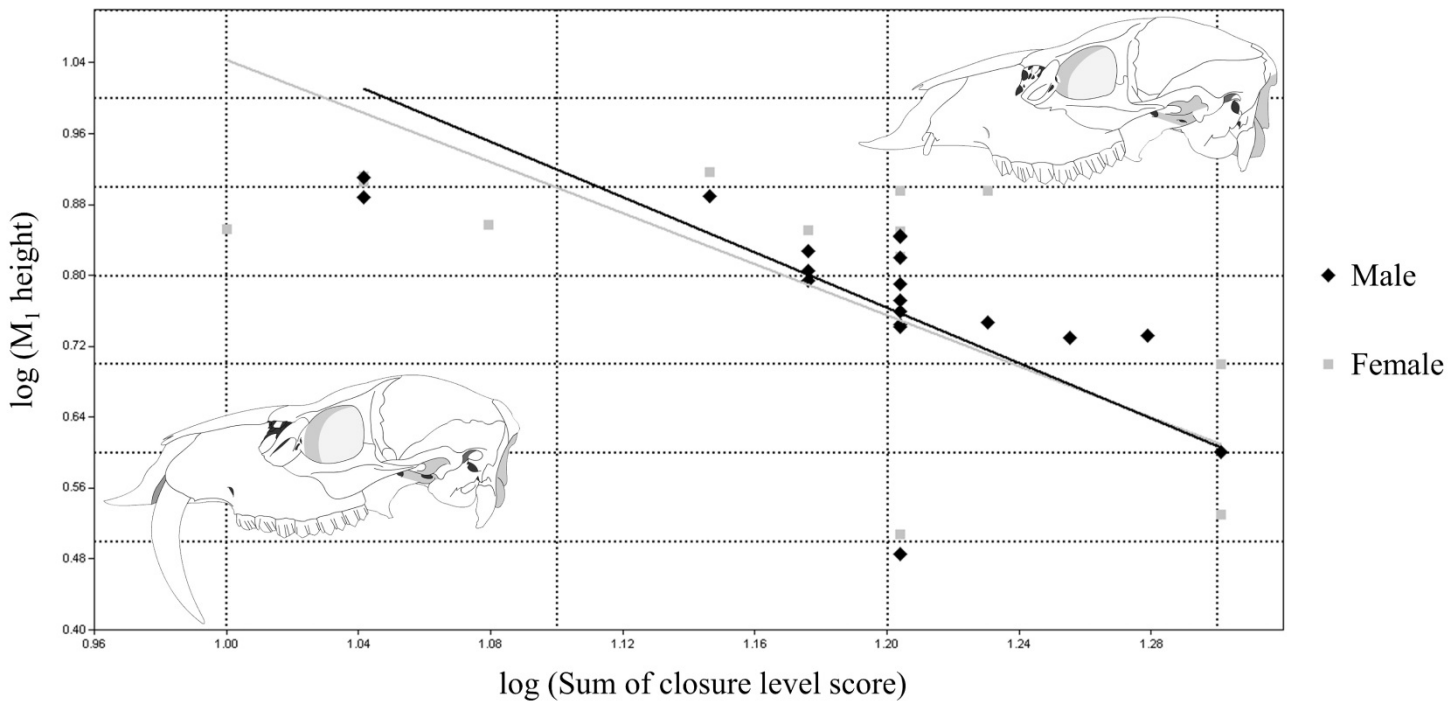

Fig. 2. Relationship between M_1 height and sum of closure level score. Black diamonds describe the plots in males, and gray squares describe those in females. Lines represent ordinary least-squares regression in males and females, respectively. The skull in the left corner represents adult male and one in the right represents adult female.

DISCUSSION

In general, tension promotes bone formation at a suture site whereas compression impedes it (Wagemans et al., 1988). Several studies observed bone formation at a cranial suture of a rat (*Rattus*) in which a tensile force was applied using an expansion device (Miyawaki and Forbes, 1987; Sasaki et al., 2002). In addition, a study with a high-pull head-gear appliance found that sutures of the facial bones in the rhesus monkey (*Macaca mulatta*) exhibited resorptive activity (Elder and Tuenge, 1974).

Given these reports and that the large canines of males used when striking their heads in male–male combat, our a prior expectation was that the difference in cranial suture closure should be found between male and female water deer. The skull of the male water deer is expected to experience more physical stress than that of the female because of such male–male combat where the canines are used. Physical stress on the skull during this behavior acts as tension or compression to the cranial sutures. Thus, this study was predicted that this will influence bone deposition on the cranial suture site of male water deer and will result in sexual dimorphism of the suture closure pattern.

However, no significant sexual dimorphism regarding suture closure pattern was observed, except for the earlier interfrontal closure in males, which is just a phylogenetic pattern shared with Capreoleinae and Alcinae (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014). Some cases report that cranial suture closure does not necessarily exhibit the predicted effect of physical stress. The nasofrontal suture of the miniature pig (*Sus scrofa*), which is influenced by compression, showed the most rapid bone growth among cranial sutures studied by Rafferty and Herring (1999). Chondroid tissue contained in the nasofrontal suture was suggested as a factor that contributed to this counterintuitive result.

Mastication seems to be one possible factor affecting the closure pattern of sutures of oral regions. Ruminant species move their lower jaws sideways during mastication. Bärmann and Sánchez-Villagra (2012) suggested this movement as a reason for ruminants, even larger species, showing less closure of cranial sutures than other artiodactyls. In their study, less than half of the studied cranial sutures in ruminant species were closed and the oral-nasal region was the least closed compared with other regions. Similarly, in the study by Rager et al. (2014), three cervid species (*Capreolus capreolus*, *Muntiacus muntjak*, and *Rangifer tarandus*) showed no closure of cranial sutures around the rostrum.

A hinged canine structure can be one of the possible reasons for the absence of the influence of canines on cranial suture closure pattern. The canines of male water deer are not tightly implanted in the socket. Furthermore, the socket is much larger than the canines (Fig. 3), and therefore, the position of the canines is not firmly fixed. Canines are embedded in soft tissue, and their position is controlled by facial muscles. This structure may decrease impact during fights using canines (Aitchison, 1946; Cooke and Farrell, 1998). Because of that shock absorption, physical stress on the skull caused by the combat behavior of male water deer may be sufficiently minimized to influence the cranial suture closure pattern.

Fig. 3. Ventral view of rostrum of male water deer. Sockets of canine teeth larger than its teeth can be identified.

Nicolay and Vaders (2006) reported shock absorption as a possible cause blurring sexual dimorphism between males and females. They studied the degree of the cranial suture interdigitation of white-tailed deer (*Odocoileus virginianus*) in which only males possess antlers. The presence of antlers did not make a significant difference in the degree of interdigitation of the cranial suture between both sexes. Antlers have greater energy-absorbing properties than ordinary skeletal bone; hence, they may decrease the mechanical strain on the cranial suture. Similarly, it is possible that because of the hinged canines, males are not required to have derived cranial suture patterns.

During this study, it was observed that the degree of interdigitation of suture around the cranium roof in water deer is smaller than that in other cervid species. Presumably, the stress pattern is more related to morphology of the suture itself than closure patterns. Difference in the degree of interdigitation depends on the polarity of sutural strain, as reported in several studies (Rafferty and Herring, 1999; Sun et al., 2004). In *Ovis orientalis*, males display more combat behavior than females and a difference in complexity in some cranial sutures is observed between the sexes (Jaslow, 1989). It was concluded that sequence of cranial suture closure is little influenced by mechanical stress and rather strongly reflect phylogeny.

CHAPTER II

Phylogenetic Pattern of Cranial Suture Closure in Cervids

INTRODUCTION

Cranial suture closure sequences of many mammal species are discovered to find its phylogenetic implication (Bärmann and Sánchez-Villagra, 2012; Goswami et al., 2013; Oh et al., 2017a; Rager et al., 2014; Wilson and Sánchez-Villagra, 2009). Closure sequences of many cervid species are also included in observation of previous studies. Currently, suture closure sequence of ten extant species and two extinct species have been reported among cervids (Bärmann and Sánchez-Villagra, 2012; Oh et al., 2017a; Rager et al., 2014). The cranial suture closure sequence of Siberian roe deer (*Capreolus pygargus*) and Sika deer (*Cervus nippon*) has been lacking. These two cervid species are representative deer species in Northeastern Asia. Comparison of these two species with other cervid species will give contribute to fill our knowledge.

Family Cervidae can be divided into telemetacarpalian group and plesiometacarpalian group. These terms are not available in formal nomenclature but they are widely used (Groves, 2007). Deer in telemetacarpalian group have second and fifth metacarpal bones which only have distal end. Those bones have only proximal end in plesiometacarpalian deer (Geist, 1998; Groves, 2007).

Plesiometacarpalian group includes species in subfamily Cervinae, and Telemetacarpalian group includes the other species (Groves, 2007). This separation is identical to molecular studies (Hassanin and Douzery, 2003; Pitra et al., 2004).

Siberian roe deer (*Capreolus pygargus*) are a cervid species distributed in southern Ural Mountains, northern and eastern Kazakhstan, Kyrgyzstan, southern Siberia, northern and central China, northern Mongolia and Korea (Grubb, 2005). Siberian roe deer specimens used in this study are from population in Jeju Island of Korea. This population has smaller size than mainland population and distinguished from mainland population by mitochondrial cytochrome b analysis. (Koh et al., 2000; Park et al., 2011; Park et al., 2014; Park et al., 2016).

Two species are currently recognized for genus *Capreolus*. The congener *Capreolus capreolus* is distributed in Europe, western Russia, Ukraine, Turkey, Caucasus region, northwestern Syria, northern Iraq and northern Iran (Grubb, 2005; Sempéré et al., 1996). *Capreolus pygargus* has been differentiated from *Capreolus capreolus* by the color of its head and metatarsal gland (Danilkin, 1995; Sempéré et al., 1996).

The genus *Capreolus* is a sister genus of the water deer (*Hydropotes*) (Pitra et al., 2004). While closely related, these two genera are morphologically very

different; male *Capreolus* has antlers but canines are absent while male *Hydropotes* lacks antlers and have well developed canines. These characteristics of *Hydropotes* are distinguished from other Cervidae species. 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). Male *Muntiacus* also possesses canines (Pitra et al., 2004; Randi et al., 1998), but molecular evidence supports that genus *Hydropotes* is closer to genus *Capreolus*, rather than *Muntiacus* (Pitra et al., 2004; Randi et al., 1998). 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* (Gilbert et al., 2006; Pitra et al., 2004; Randi et al., 1998) (Fig. 4). 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.

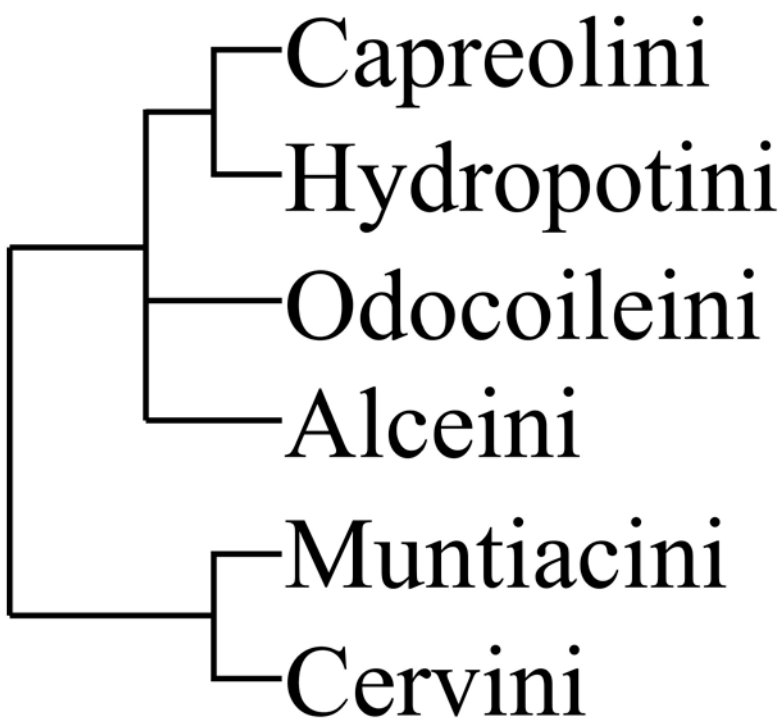

Fig. 4. Phylogenetic tree of cervid tribes based on study of Gilbert et al. (2006).

Sika deer (*Cervus nippon*) belong to tribe Cervini in family Cervidae (Groves, 2007). Sika deer are distributed in Ussuri district of southeastern Siberia, Manchuria, Korea, northern Vietnam, Japan, Ryukyu islands, Taiwan, and most of China to east of Tibetan Plateau (Nowak, 1999). Sika deer specimens used in this study are from Japan. Japanese sika deer are classified into six subspecies: *C. n. yesoensis*, *C. n. centralis*, *C. n. nippon*, *C. n. mageshimae*, *C. n. yakushimae* and *C. n. keramae* (Ohtaishi, 1986). Populations of mainland and Kinkazan Island of Japan used in this study belong to *C. n. centralis*. Molecular studies also show that two populations are genetically close (Tamate et al., 1998).

Sika deer are morphologically highly similar with red deer (*Cervus elaphus*) and have close phylogenetic relationship with red deer in tribe Cervini (Kuwayama and Ozawa, 2000; Pitra et al., 2004). Male sika deer are generally larger than females in skull and body size. Feldhamer (1980) reported that body and cranial measurements of male sika deer each averaged 8.7% and 8.9% larger than those of females. Body weight was also larger in males (Feldhamer, 1980). Uchida et al. (2001) found that increase rates in body weight of sika deer are same in both sexes until three months after birth, but it becomes greater in males than females after four months. Increase of condylobasal length of male sika deer which represent

general skull growth completed by the fourth year in study of Hayden et al. (1994). Maximum growth of antler is acquired after sixth year (Hayden et al., 1994).

Here, cranial suture closure patterns of Siberian roe deer in Jeju Island of Korea and Japanese sika deer are examined to describe their characteristics and differences from other cervid species.

MATERIALS AND METHODS

Skull specimens of Siberian roe deer studied here were all collected from Jeju island of Korea and stored at the College of Veterinary Medicine, Chonbuk National University (Iksan, South Korea), Department of Science Education, Jeju National University (Jeju, South Korea), Folklore and Natural History Museum (Jeju, South Korea), Halla Arboretum (Jeju, South Korea) and the Roe Deer Observation Center (Jeju, South Korea). Twenty four male and seven female Siberian roe deer specimens were observed. Detailed information can be found in Table 3.

Table 3. Closure levels observed in cranial sutures of Siberian roe deer specimens

Specimen Number	Sex	Exoccipital-Basioccipital	Supraoccipital-Exoccipital	Basisphenoid-Basioccipital	Interparietal	Presphenoid-Basisphenoid	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-Palatine	Basisphenoid-Temporal	Interfrontal	Frontal-Parietal	Parietal-Temporal	Parietal-Supraoccipital	Temporal-Supraoccipital	Temporal-Exoccipital	Total cranial Length (mm)	Viscerocranium Length (mm)	Neurocranium Length (mm)	Collection
JNU001	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	181.84	92.25	108.84	JNU
JNU002	F	4	4	4	4	4	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	97.12	JNU
CNU-Jeju007	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	178.23	93.41	109.10	CNU
RDOC001	F	4	4	4	4	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	106.10	RDOC
CNU-Jeju008	F	4	3	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	106.63	CNU
080802	F	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	180.94	98.66	108.22	JNU
CNU-Jeju006	F	4	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	87.49	CNU
RDOC004	M	4	4	3	4	4	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	185.45	106.97	108.77	RDOC
FNHM002	M	4	4	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	192.24	102.18	116.60	FNHM
CNU-Jeju004	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	186.26	100.52	111.33	CNU
CNU-Jeju012	M	4	4	4	4	0	-	-	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	110.68	CNU
JNU003	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	190.12	102.39	115.88	JNU
JNU004	M	4	4	4	4	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	117.23	JNU
FNHM001	M	4	4	4	4	0	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	109.20	FNHM

Table 3. continued

RDOC002	M	4	4	4	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	185.64	99.87	113.42	RDOC
RDOC007	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	185.78	95.80	112.62	RDOC
RDOC008	M	4	4	4	4	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	108.39	RDOC
RDOC009	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	187.65	97.21	112.48	RDOC
CNU-Jeju005	M	4	3	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	183.44	101.07	113.54	CNU
FNHM004	M	4	4	4	3	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	-	-	-	FNHM
FNHM003	M	4	4	1	4	0	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	111.25	FNHM
CNU-Jeju001	M	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	193.81	107.16	112.59	CNU
HA002	M	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	187.20	100.35	111.47	HA
RDOC003	M	4	4	4	0	0	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	109.73	RDOC
HA001	M	4	4	3	0	0	-	-	-	-	-	-	-	-	-	0	-	0	0	0	0	-	0	0	0	0	0	0	0	-	-	106.85	HA
JNU005	M	4	4	0	4	0	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	101.32	JNU
HA003	M	4	4	0	4	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	113.54	HA
RDOC005	M	4	4	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	109.73	RDOC
RDOC006	M	4	4	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	115.74	RDOC
CNU-Jeju003	M	4	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	89.81	CNU
HA004	M	2	3	0	4	0	-	-	-	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	113.25	HA

M=Male, F=Female; Closure level score : 0 (not fused), 1 (¼ fused), 2 (½ fused), 3 (¾ fused), and 4 (totally fused).
"-" indicates missing data due to fracture of specimens. Abbreviations: JNU, Department of Science Education, Jeju National University (Jeju, South Korea); CNU, College of Veterinary Medicine, Chonbuk National University (Iksan, South Korea); RDOC, Roe Deer Observation Center (Jeju, South Korea); FNHM, Folklore and Natural History Museum (Jeju, South Korea); HA, Halla Arboretum (Jeju, South Korea).

Skull specimens of *Cervus nippon* from mainland of Japan stored in Kanagawa Prefectural Museum of Natural History and those from Kinkazan Island stored in Azabu University were used for this study. In total, 78 male specimens, 69 female specimens and three juvenile specimens with unknown sex were studied. Detailed information can be found in Table 4.

Table 4. Closure levels observed in cranial sutures of Japanese sika deer specimens

Specimen Number	Sex	Interparietal	Exoccipital-Basioccipital	Supraoccipital-Exoccipital	Basisphenoid-Basioccipital	Presphenoid-Basisphenoid	Orbitosphenoid-Palatine	Orbitosphenoid-Frontal	Parietal-Supraoccipital	Interincisive	Incisive-Maxillary	Internasal	Nasal-Maxillary	Intermaxillary	Maxillary-Lacrimal	Maxillary-Palatine	Maxillary-Zygomatic	Interpalatine	Lacrimal-Zygomatic	Nasal-Frontal	Lacrimal-Frontal	Zygomatic-Frontal	Zygomatic-Temporal	Alisphenoid-Parietal	Alisphenoid-Temporal	Interfrontal	Frontal-Parietal	Parietal-Temporal	Temporal-Supraoccipital	Temporal-Exoccipital	Total length (mm)	Viscerocranium Length (mm)	Median frontal Length (mm)	Collection
007-1215	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	298.0	150.0	158.6	KPMNH
607-1129	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	195.0	89.8	113.4	KPMNH
607-167	M	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	292.5	143.4	159.1	KPMNH
607-168	F	4	4	4	4	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	268.4	134.6	144.9	KPMNH
2066	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	257.8	131.9	135.7	KPMNH
2068	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	266.7	132.9	140.9	KPMNH
2069	M	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	261.3	127.5	142.2	KPMNH
2071	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	256.6	127.7	137.4	KPMNH
2072	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	254.8	126.2	137.3	KPMNH
2076	F	4	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	262.3	129.9	142.3	KPMNH
2078	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	268.9	128.6	148.7	KPMNH
2079	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	254.5	127.8	135.8	KPMNH

Table 4. continued

2081	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	257.7	125.8	139.6	KPMNH
2082	M	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	250.2	115.5	145.5	KPMNH
2084	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	199.2	76.7	128.8	KPMNH
2086	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	246.3	124.4	130.7	KPMNH
2087	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	265.7	135.9	138.6	KPMNH
2112	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	251.4	114.7	146.1	KPMNH
2178	F	4	4	4	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	266.3	134.4	141.0	KPMNH
2203	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	194.7	86.3	116.2	KPMNH
2204	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	201.8	87.0	122.2	KPMNH
2206	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	208.8	94.9	123.4	KPMNH
2328	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	283.3	141.7	150.1	KPMNH
2332	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	252.6	121.1	141.2	KPMNH
2334	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	196.0	86.1	117.2	KPMNH
2339	M	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	261.5	115.4	153.9	KPMNH
2341	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	235.0	108.8	133.8	KPMNH
2342	F	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	255.8	125.3	140.8	KPMNH
2534	M	4	4	4	4	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	294.3	144.1	159.9	KPMNH
2602	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	299.2	147.0	162.7	KPMNH
2603	M	4	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	268.3	135.5	142.8	KPMNH
2604	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	235.5	109.4	134.4	KPMNH
2605	F	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	208.2	92.0	123.0	KPMNH

Table 4. continued

| | | |

Age variation of cranial suture closure pattern is described in Table 11. Description of cranial suture closure patterns are summarized as closure degree of five cranial sutures which show variation of closure degree. Interparietal, supraoccipital-exoccipital, basisphenoid-basioccipital, presphenoid-basisphenoid and orbitosphenoid-palatine sutures showed variation of closure degree. Patterns will be described as closure level scores arranged as this order after here. Age of pattern 40000 varied from 0 to 4 years old. Age of pattern 43000 varied from 2 to 5 years old. Age of pattern 43400 varied from 4 to 11 years old. Age of pattern 44400 varied from 6 to 10 years old. Age of pattern 44410 varied from 6 to 13 years old. Other patterns also existed but number of specimens is not enough to generalize the result.

Table 11. Age variation of cranial suture closure pattern in sika deer of Kinkazan Island

Interparietal		3		4		4		4		4		4		4		4		4		4		4		4		4		4		4		4		
Supraoccipital-Exoccipital		0		0		1		2		3		3		3		3		3		3		4		4		4		4		4		4		
Basisphenoid-Basioccipital		0		0		0		0		0		0		1		4		4		4		0		0		4		4		4		4		
Presphenoid-Basisphenoid		0		0		0		0		0		1		0		0		1		0		3		4		0		0		1		4		n
Orbitosphenoid-Palatine		0		0		0		0		0		0		0		0		0		2		0		0		0		1		0		0		
Sex		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
	0 - 1		1	5	5																													11
	1 - 2			6	3																													9
	2 - 3			9	3					1																								13
	3 - 4			1		1				2	1			1																				6
	4 - 5									1	1					2																		4
	5 - 6															1	2			1														4
Age	6 - 7							1								6	1							3				1						12
	7 - 8											1				4	1							1										7
	8 - 9															3		1					1	1										6
	9 - 10															2	2									1		1	1					7
	10 - 11																1					1												2
	11 - 12																										1	1			1			3
	12 - 13																	1										2						3
n		1		32		1		1		6		1		1		25		2		1		1		1		6		1		6		1		

M=Male, F=Female; Cells with gray color show sutures which closed more than half.

Blind test of specimen 2079 and 2086 failed to predict their age. Estimated ages by cementum annuli of specimen 2079 and 2086 were 5.5 and 5.0 years old. The specimens were females and their cranial suture closure pattern was 44400. In result of this study, age of pattern 44400 in female varied from 9 to 10 years old. But this result is not reliable because pattern 44400 in female was observed in only one specimen (Nishinu). More observation data is needed to ensure the result.

Blind test of specimen 2069 and 2082 predicted their age. Estimated ages by cementum annuli of specimen 2069 and 2082 were 3.5 and 3.0 years old. The specimens were males and their cranial suture closure pattern was 43000. Age of pattern 43000 in males in this study varied from 2 to 5 years old. This data was acquired from four specimens (MG84-97, MG84-133, MG84-190 and MG84-240).

DISCUSSION

This study examined if the degree of suture closure is correlated with age and assessed the validity of the degree of suture closure for age estimation in cervid species. Based on sika deer specimens from Kinkazan Islands of Japan, this study found that the suture closure scores strongly reflect actual aging.

Dental layers of teeth are often used to estimate absolute age in mammals (Altmann et al., 1981; Anders et al., 2011; Calvert and Ramsay, 1998; Dietz et al., 1991; Hartman, 1995; Hewison et al., 1999; Hillman-Smith et al., 1986; Hohn et al., 1989; Marmontel et al., 1996; Morris, 1972; Oliveira et al., 2007; Sharman et al., 1964; Spinage, 1972; Stander, 1997; Van Jaarsveld et al., 1987). In cervids, this method can be applied to all ages, because first white cement layer in teeth is deposited in one year since birth (Mitchell, 1967). Age estimation in deer by dental layers has been extensively studied by Hamlin et al. (2000). Counting the yearly deposition of white and translucent layers allows detailed determination of age (Mitchell, 1967). The problem of this method is that this inevitably involves destruction of precious specimens. First incisor should be sliced for observation of dental layers (Hamlin et al., 2000). This problem makes it difficult to apply age

estimation by counting dental layer when researchers have to use specimens collected by museums. It is difficult to get permission from collection managers to destroy specimens. If specimens are from rare or extinct species, getting permission is almost impossible.

In this case, non-invasive methods should be used although they are not accurate as counting dental layers. There are some estimation methods to avoid destruction such as observing branching pattern of antler, tooth replacement or tooth wear. (Hayden et al., 1994; Hewison et al., 1999; Koike and Ohtaishi, 1985; Kubo and Yamada, 2014; Meindl and Lovejoy, 1985; Morris, 1972; Ozaki et al., 2010). However, as noted earlier, these methods are only applicable to one sex, or young individuals or specific population. In this regard, cranial sutures, which can be observed in both sexes regardless of maturity, possess the potential to be an alternative non-destructive approach for age estimation.

This study confirmed that correlations between suture closure level and age were stronger than those between skull lengths and age. It was also even stronger than correlations between M_1 crown height and age, which has been frequently used as age criterion in previous studies. This strong correlation supports potential of cranial suture closure as age indicator.

Cranial suture exist in both sexes, so age of both sexes can be estimated by cranial suture. It seems that method should be made in males and females separately. The closure sequences were comparable between both sexes. Cranial sutures of sika deer skull closed as order of interparietal suture, sutures around foramen magnum, and then sutures in basicranial region. But closure timings of some sutures were different between both sexes. Especially, closure timing of presphenoid-basisphenoid suture was earlier in females than males. It was found that regression slopes overlapped between both sexes, but slope of males is little higher than that of females. Sexual differences in suture closures are also known for humans. In humans, it is reported that cranial sutures shows stronger correlation with age in females than in males (Key et al., 1994).

Closure sequence was virtually identical between mainland and Kinkazan Island populations with little variation. Although only two populations were studied in this study, this result suggested limited geographic variation of suture closure sequence in this species. According to Ohtaishi (1986), there are six subspecies in Japanese sika deer: *C. n. yesoensis* in Hokkaido Island, *C. n. centralis* in Honshu mainland and Tsushima Island, *C. n. nippon* in Kyushu Island, Shikoku Island and Goto Islands, *C. n. mageshimae* in Mageshima Island and Tanegashima

Island, *C. n. yakushimae* in Yakushima Island and Kuchinoerabu Island and *C. n. keramae* in Ryukyu Islands. Molecular studies divide Japanese sika deer into northern and southern lineages (Nagata, 2009; Nagata et al., 1999; Tamate et al., 1998). Northern lineage includes *C. n. yesoensis* and *C. n. centralis* in Honshu mainland except for south-western part. Mainland population and Kinkazan Island population are taxonomically in same subspecies (*C. n. centralis*) and genetically in same northern lineage (Tamate et al., 1998). Despite of these similarities, two populations show morphological difference. Kinkazan Island population has smaller size and weight than mainland population (Kubo and Takatsuki 2015; Ozaki et al., 2010). Because of high population density and food limitation, Kinkazan Island population should consume short grass and fallen leaves and ingest soil and grit with them. This environment makes their molar wear rate faster than mainland population (Kubo et al., 2011; Ozaki et al., 2010). So age estimation by molar wear rate has difficulty to be commonly applied to two populations. However, result of this study showed same cranial suture closure sequence between two populations and suggested that age estimation by suture closure sequence is able to be applied to different populations. Blind test also provided same conclusion. Closure pattern acquired from Kinkazan Island population predicted

age of two male specimens of mainland population successfully. Unfortunately, difference of timing is not able to be assessed because only four specimens from the mainland of Japan used in this study have information on age. In case of human, suture closure timing is slightly different between different populations (Key et al., 1994). Although limited number of specimens is available for sika deer, further studies on individuals from other regional populations with age information will contribute to improve the accuracy of age determination by cranial suture closure.

Age of old specimens also can be estimated by cranial suture closure. Overall cranial suture closure degree increased even in old ages. Among specimens with age information, female specimen of age 11.5 years old recorded 20 which is the highest sum of closure level scores. However, some specimens with no age information recorded more than 20. It means sum of closure level scores increases even after 11.5 years old. Maximum life span of artificially raised Japanese sika deer is 26 years (Ohtaishi, N. 1978). But generally, age estimation is needed for specimens of wild animals. In wild populations, maximum life span is 16 years (Ohtaishi, N. 1978). 11.5 years old is quite old age in wild populations. Studies on humans also pointed out that cranial sutures is powerful especially in estimating old ages because postcranial age indicators such as pubic suture closures may lose

accuracy particularly in elder specimens (Meindl and Lovejoy, 1985).

However, there are several questions that need to be addressed by further studies. Estimated range of age is quite broad. It is also pointed out in study of humans (Key et al., 1994). It is impossible to assign specific age in years. The maximum range was distributed from 4 years old to 11 years old in pattern 43400. In further studies, specimen numbers should be increased and confirm that in what age each patterns are mainly distributed.

The results also call out attention to individual variation of suture closure. It is known that humans show individual variation of suture closure pattern. In particular, delayed closures of cranial sutures are often observed. This type of delay is observed in both sexes, but especially more in males (Key et al., 1994). In this study, two male specimens (5.37 and 11.5 years old) showed partial closure of the orbitosphenoid-palatine suture, which was not closed in any other specimens. This kind of rarely observed variations would overestimate the age. This suggests that screening sutures which have less variation and higher relationship with age is the next essential step to refine this non-invasive approach.

In conclusion, findings of the present study highlight the validity of age estimation by cranial sutures. The cranial suture closure of sika deer shows strong

relationship with age. Age can be inferred by the formula in males and in females. Age estimations by cranial suture closure levels are equally powerful to or even more powerful than other non-destructive estimation methods. This study points out that cranial suture closure pattern will be a strong alternative for non-destructive age determination. Combined application of cranial suture closure pattern with other existing indicators will contribute to more accurate age determination.

GENERAL CONCLUSION

To confirm reflection of physical stress, phylogenetic relationship and growth on cranial suture closure pattern of cervids, three studies are conducted and following results are acquired.

Cranial suture closure pattern of water deer (*Hydropotes inermis*) was provided and compared between both sexes. Difference was closure of interfrontal suture only in males. It seemed not to be related with prominent canine teeth which exist only in males and expected to be related with phylogenetic pattern in cervids. Biomechanical factor may be little related to cranial suture closure sequence of water deer. Morphology of individual suture might give better comprehension between suture and mechanical stress.

Cranial suture closure patterns of Siberian roe deer (*Capreolus pygargus*) in Jeju Island and sika deer (*Cervus nippon*) in Japan were provided and phylogenetic pattern among Cervidae was assessed by comparing cranial suture closure sequences. Patterns like variation rate and number of closing sutures can be unique pattern of species or clade. Genus *Capreolus* commonly showed variation of interparietal suture closure timing and was suggested that the intraspecific variation

of interparietal suture closure timing is derived character of *Capreolus*. Reduced closure of cranial suture is considered as evolutionary tendency of *Cervus nippon*.

Relationship between cranial suture closure pattern of sika deer (*Cervus nippon*) and age was provided. Age information was available because observed specimens have extensive life records. Relationship was strongly positive and even stronger than relationship between age and first molar height which frequently used as age indicator in other studies. This result showed potential of cranial suture closure pattern as age indicator.

Studied deer species commonly showed closure of interparietal, exoccipital-basioccipital, supraoccipital-exoccipital, basisphenoid-basioccipital and presphenoid-basisphenoid sutures. In most of species, cranial sutures closed as this order. Based on data of sika deer in Kinkazan Island, cranial suture closure pattern is deeply related with growth. Interparietal and exoccipital-basioccipital sutures close in fawns (age < 1 years old), supraoccipital-exoccipital and basisphenoid-basioccipital sutures close in young adults (age more than two years old and less than 4 years old), and presphenoid-basisphenoid sutures close in adults (age > 4 years old). Some cervid species showed additional closures of cranial sutures. Morphological differences like large canines could not explain the variation of

pattern. Considering previous studies (Bärmann and Sánchez-Villagra, 2012), other morphological differences like body mass or antler size also could not completely explain the variations. In previous studies, several mammal species showed possible relationship between cranial suture closure pattern and physical stress caused by morphological and behavioral features (Bärmann and Sánchez-Villagra, 2012; Rager et al., 2014). However, in cervids, morphological or behavioral features seem to have little effect to cranial suture closure pattern. Phylogenetic relationship among Cervidae is highly reflected in variation of cranial suture closure pattern like other mammal clades (Bärmann and Sánchez-Villagra, 2012; Goswami et al., 2013; Rager et al., 2014; Wilson and Sánchez-Villagra, 2009).

Results of this study presented usefulness of cranial suture closure pattern in study of cervids. Phylogenetic pattern of cranial suture closure can contribute to classification of cervids. Classification of subfamily Cervinae is controversial especially in genus *Cervus*. Further studies with many species will provide morphological evidences needed for classification. Relationship between age and cranial suture closure pattern will provide more convenient method for age determination. In this study, cranial suture closure pattern showed positive relationship with age even stronger than that of other non-invasive methods for age

estimation. Improvement by further studies and combination with other age determination methods will contribute to other studies using skull specimens.

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사슴류에서 머리뼈봉합의 유합 양상 분석 및 이를 통한 비침습적 연령추정법 개발

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국문초록

머리뼈봉합은 머리뼈를 구성하는 뼈들이 만나는 곳에 존재하는 섬유조직이다. 어린 동물의 머리뼈를 구성하는 뼈 가장자리에서 일어나는 뼈의 성장은 머리뼈봉합이 존재함으로써 가능하다. 동물이 성숙하면

머리뼈봉합은 골화되어 사라진다. 머리뼈봉합의 유합 시기는 각 머리뼈봉합마다 달라 고유의 유합 양상이 만들어지고, 이것은 많은 포유동물 종에서 다양하게 나타난다. 머리뼈봉합의 유합 양상은 포유류의 성장, 행동 양식, 진화 양상 등을 반영하기 때문에 머리뼈봉합의 유합에 대한 비교 연구는 그에 대한 유용한 정보를 제공할 수 있다. 본 연구에서는 동북아시아에 서식하는 3종의 사슴류의 머리뼈봉합 유합 양상을 관찰하고 이것이 사슴과(科) 동물에서 갖는 의미를 살펴볼 것이다.

제 1 장에서는 한국의 고라니(*Hydropotes inermis*)의 머리뼈봉합 유합 양상을 관찰하였다. 고라니는 진화를 통해 뿔을 잃었다는 것에서 사슴류 중 매우 예외적인 동물이다. 수컷은 암컷과 달리 발달된 송곳니가 존재하고, 이것을 수컷끼리의 싸움에 이용한다. 이 특유의 형태적 특징이 본 연구로 하여금 발달된 송곳니의 유무가 머리뼈봉합의 유합에 영향을 주는 지를 평가하게 하였다. 연구 결과, 고라니에서 머리뼈봉합의 유합 순서는 송곳니와의 관계가 미미한 것으로 나타났다. 고라니의 송곳니는 송곳니에 비해 상대적으로 큰 이틀 안에서 물렁조직 속에 파묻혀있고 이에 의해 물리적 충격이 완화된다. 큰 물리적 충격이 예상되는 특이한 행동 양상이 있더라도 이것이 반드시 머리뼈봉합의

유합 양상에 영향을 미치지는 않았다.

제 2 장에서는 제주도에 서식하는 시베리아노루(*Capreolus pygargus*)와 일본에 서식하는 일본사슴(*Cervus nippon*)의 머리뼈봉합 유합 양상을 관찰하고 현존하는 11종의 사슴류에서 머리뼈봉합의 유합 양상을 비교하였다. 변이의 발생율이나 유합되는 봉합의 수와 같은 유합 양상도 종이나 분류군을 구분지었다. 마루뼈사이봉합의 유합시기는 시베리아노루 종에서 매우 다양하게 관찰되었다. 유럽노루(*Capreolus capreolus*) 역시 마루뼈사이봉합의 유합 시기가 유사한 변이를 보였으나, 다른 사슴류에서는 이러한 변이가 관찰되지 않았다. 마루뼈사이봉합 유합의 높은 종내 변이율은 *Capreolus* 속(屬)의 후천적 특징으로 생각되었다. 일본사슴을 제외한 다른 사슴족(族)의 종들은 사슴류에서 공통적으로 유합되는 다섯 개의 머리뼈봉합 이외의 다른 머리뼈봉합들도 추가적인 유합이 관찰되었다. 일본사슴은 해당 머리뼈봉합들의 추가적인 완전한 유합을 보이지는 않았지만, 부분적인 유합은 관찰되었다. 일본사슴의 진화는 머리뼈봉합의 유합을 줄이는 방향으로 이루어진 것으로 보였다.

제 3 장에서는 일본의 긴카산 섬에 서식하는 일본사슴(*Cervus nippon*)의 머리뼈봉합 유합 순서와 연령의 상관관계를 평가하였다.

마루뼈사이봉합과 가쪽뒤통수뼈-바닥뒤통수뼈봉합은 생후 1년 내에 닫혔고, 위뒤통수뼈-가쪽뒤통수뼈봉합과 바닥나비뼈-바닥뒤통수뼈봉합은 어린 성체에서 닫혔고, 앞나비뼈-바닥나비뼈봉합은 나이든 성체에서 닫혔다. 머리뼈봉합 유합 수준 점수의 합과 연령은 높은 정적 상관관계를 나타냈다. 이것은 심지어 일반적으로 많이 쓰이는 비파괴적 연령 추정 방법인 아래턱 첫째 큰어금니와 연령 사이의 관계보다도 더욱 높았다. 본 연구의 결과, 일본사슴의 연령은 수컷에서 $0.8296 \times$ (머리뼈봉합 유합 수준 점수의 합) $- 4.8482$, 암컷에서 $0.8892 \times$ (머리뼈봉합 유합 수준 접수의 합) $- 5.5923$ 으로 추정해볼 수 있음이 제시되었다. 이 연구에 이용된 87점의 표본 중 82점의 표본의 연령이 위 회귀식의 95% 신뢰구간 내에서 예측되어 머리뼈봉합을 이용한 연령 추정은 높은 신뢰도를 보였다. 머리뼈봉합을 이용한 연령추정은 기존에 존재하는 다른 연령추정 방법들과 비교했을 때 암수 모두에 적용 가능하고, 나이든 표본의 연령도 추정할 수 있다는 장점이 있었다. 이 연구는 머리뼈봉합 유합 양상이 연령 추정의 유용한 대안으로서의 그 가능성을 강조한다.

머리뼈는 그 종의 생태적, 계통발생학적 특징이 반영되어 있기 때문에 포유류의 형태학적 연구에서 빈번히 이용되는 매우 중요한 표본이다. 이

때문에 머리뼈에 대한 이해는 형태학적 연구에 있어서 중요하다. 머리뼈의 중요한 구조 중 하나인 머리뼈봉합에 대한 이해는 그 종의 계통발생학적 관계와 생태적 특징을 연구하는 데 도움을 줄 것이다. 연령 정보 역시 포유류의 연구에서 매우 중요한 정보이다. 성장 양상, 번식 양상 등의 연구에 있어 연령은 필수적인 정보이다. 그 때문에 더욱 많은 지표를 이용하여 연령을 정확히 추정할 수 있다면 많은 연구에 기여할 수 있을 것이다. 머리뼈봉합에 대한 이해와 그를 이용한 연령 추정은 그 종의 연구에 많은 중요한 정보를 제공할 것이다. 본 연구의 결론은 사슴류의 머리뼈봉합 유합 양상은 나이와 깊은 관계가 있으며, 종 사이에서 유합 양상의 차이는 물리적 자극이나 형태적 특징보다는 계통발생학적 관계에 더 영향을 받는다는 것이다. 또한 사슴류의 연령은 머리뼈봉합의 유합 양상을 통해 표본의 손상 없이 추정이 가능하다는 것이다. 이 연구의 결과는 미래의 사슴류 연구에 기여할 것이다.

주요어: 고라니, 머리뼈봉합, 머리뼈, 시베리아노루, 일본사슴

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