

博士論文（要約）

Evolution of musculoskeletal structure of neck in artiodactyls
(偶蹄類における頸部筋骨格構造の進化)

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Chapter 1

General introduction

General introduction

Vertebrates had gained a 'neck' as a byproduct of the acquirement of the prototype of the forelimb that helped to support the body weight and to walk in the terrestrial life (Clack 2012). In the teleost fishes, the pectoral girdle is a part of the skull attached to the gill and throat bones (Fig. 1-1a; Benton 2014). In the taxa that are related to the fish-tetrapod transition, *Tiktaalik*, *Acanthostega*, and *Ichthyostega*, the pectoral girdle is separated from the skull (Fig. 1-1b). This separation expands the range of the motion of the forelimb and results in the nuchal gap between the skull and pectoral girdle regarded as the origin of the neck in the vertebrate.

The neck enables animals to move their head without moving their whole body (Gans 1992). The head has the visual organ (eyes), olfactory apparatus (nose), auditory organ (ears), masticatory apparatus (mouth and teeth). Thus, the position and direction of the head are of great importance in the foraging and cognitive behaviors. The neck allows animals to face their sensory organs to an object regardless of the orientation of their body, which facilitates the sensory abilities of animals. The acquisition of neck contributes to an effective detection of a prey or predator (Gans 1992). It had prompted the diversification of the pattern of the foraging and cognitive behaviors (Wilkinson and Ruxton 2012). In spite of the evolutionary importance of the neck, little attention has been given to the evolution and development of the neck of the vertebrae over the last 150 years (Ericsson et al. 2013). There have been lots of studies on the evolution and development of the head and limbs, but little on the region between the head and forelimb. Recently, the studies get advanced in the understanding the developmental and genetic

mechanisms of the neck of model animals in the field of the experimental embryology (Bismuth and Relaix 2010; Kelly 2010; Sambasivan et al. 2011). It has led to an awakened interest in the study of the neck.

The elongation of the neck is one of the most attractive themes in the evolutionary biology. The long-necked animals have been evolved independently more than once across a wide range of both extant and extinct taxa (Wilkinson and Ruxton 2012). The long neck had produced various evolutionary advantages through the evolution of the tetrapod; therefore, many studies have attempted to clarify the evolutionary pressures underlying the neck elongation (Darwin 1871; Simmons and Scheepers 1996; Ward et al. 2008; Mitchell et al. 2009; Simmons and Altwegg 2010; Taylor et al. 2011). Additionally, the elongation of the neck has intrigued paleontologists since the extinct taxa of reptiles included lots of long-necked species (Parrish 2006; Dzemski and Christian 2007; Sander and Clauss 2008; Müller et al. 2010; Taylor et al. 2011; Stevens 2013). However, there are still very few studies on the musculoskeletal structure of the neck. The muscular system significantly affects the kinematics of the neck, and the skeletal system is the foremost important factor to influence the length of the neck. Thus, the traditional anatomical and morphological descriptions of the neck in the extant animals would give a valuable insight into the understanding of the musculoskeletal mechanism as a structural basis to determining the length of the neck.

In birds and reptiles, the elongation of the neck arises from both the increment of the number of cervical vertebrae and elongation of each vertebra (Woolfenden 1961; Taylor and Wedel 2013a). It complicates the comparison of the musculoskeletal structure

of the neck between the species in these taxa. In contrast, in mammals, the number of cervical vertebrae is almost fixed to seven due to a rigorous genetic constraint (Galis 1999; Narita and Kuratani 2005; Galis et al. 2006). This constraint makes it easy to compare the muscular and skeletal system between the species. Thus, the comparative study of the mammalian neck helps us to comprehend the musculoskeletal evolution in associated with the neck elongation.

In the present thesis, I focused on the order Artiodactyla (Mammalia) that is one of the most diverse groups in the mammal. The length and flexibility of the neck have been dramatically diversified in this taxonomic group. It contains the long-necked animals in the following three families: Giraffidae, Camelidae, and Bovidae (Wilkinson and Ruxton 2012). The family Giraffidae is the representative species in the study of the evolution of the neck. Many studies have tried to prove the evolutionary history of the extraordinary long neck of the giraffe (*Giraffa camelopardalis*) from a viewpoint of behavioral biology, morphology, anatomy, genetics, and paleontology (Leuthold and Leuthold 1972; Young and Isbell 1991; Cameron and du Toit 2005; Mitchell et al. 2013; Danowitz et al. 2015; Agaba et al. 2016; Basu et al. 2016). The family Camelidae containing various long-necked species was taxonomically diversified during the Miocene (Honey et al. 1998), and consists of six extant species that possesses relatively long neck. All of them typically prefer to eat by grazing rather than by browsing a high foliage (Matthews 1971; MacDonald 2001), making it less likely that the feeding requirement is the primary factor of selection for a long neck in the Camelidae. It implies that the long neck has evolved in the Camelidae by another evolutionary reason different

from the giraffe (Wilkinson and Ruxton 2012). The family Bovidae mainly consists of the species with short neck; hence this group had not attracted much attention in the studies investigating the evolution of neck elongation. The tribe Antilopini is the one of the diverse groups in the Bovidae (Bärmann et al. 2013) and contains three long-necked species: gerenuk (*Litocranius walleri*), dama gazelle (*Nanger dama*), and dibatag (*Ammodorcas clarkei*). Since this taxonomic group comprises various species with different neck lengths, the previous studies about the neck in the giraffe made mention of the importance to investigate the relationships between the skeleton and length of the neck in the Antilopini (Solounias 1999; Badlangana et al. 2009).

Here, I attempted to reveal the musculoskeletal adaptation in relation to the neck elongation in the artiodactyls by focusing on the Giraffidae, Camelidae, and Bovidae. The Chapter 2 is the comparative osteological study about the diversity of the neck length. I evaluated the scaling pattern of the cervical vertebrae in the longest-necked species, gerenuk, and compared them with the 13 other Antilopini species, the giraffids, and the camelids, respectively. The Chapter 3 is the comparative anatomical study of the neck in the long-necked artiodactyls. I clarified the muscular structure of the neck of the giraffe, dromedary (*Camelus dromedarius*), llama (*Lama glama*), and alpaca (*Vicugna pacos*). Then I examined the muscular adaptation to the neck elongation, by comparing these with the Sika deer (*Cervus nippon*) regarded as a species with ordinary length of the neck. In Chapter 4, I reported the specialized musculoskeletal structure of the neck of the giraffe. Then I pointed out that the giraffe moved its neck to dorsoventral direction in a significantly unique way. I revealed the evolutionary and functional insights of the

specialized neck structure of the giraffe. In Chapter 5, I summarized the above studies and then discussed the evolutionary background of the neck elongation in the tetrapod.

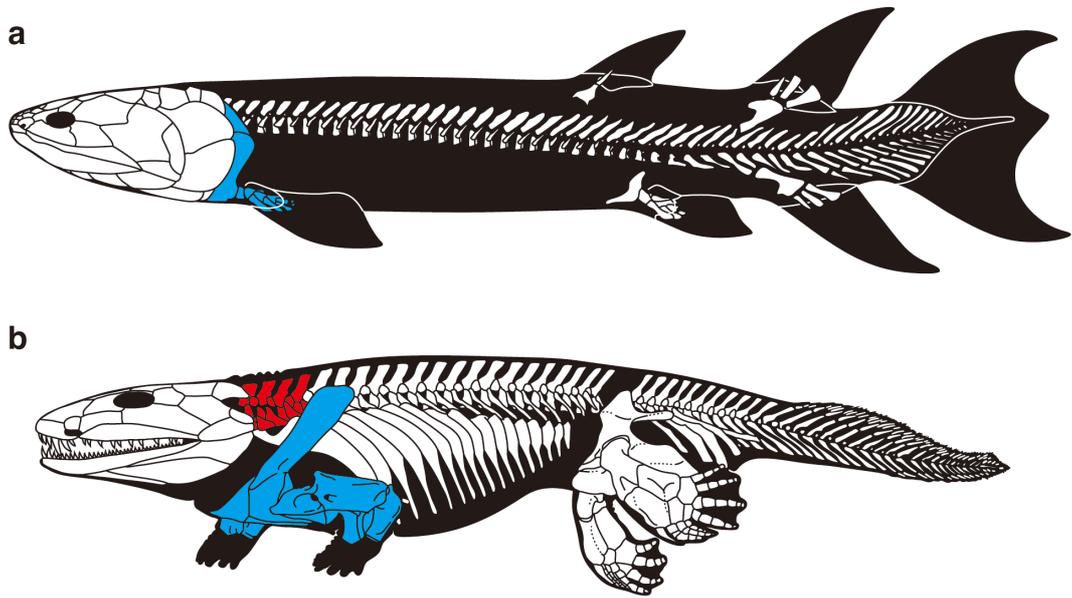


Fig. 1-1 Schematic of the skeleton in the *Eustenopteron* (a) and *Ichthyostega* (b). The region colored by blue shows the pectoral girdle and the region colored by red represents the cervical area. Adapted from the Benton (2014, Fig. 4. 6 (a), (d)).

Chapter 2, Chapter 3 の内容は、学術雑誌論文として出版する計画があるため公表できない。5年以内に出版予定。

Chapter 4

Functional cervicothoracic boundary modified by anatomical shifts in the neck of giraffe

Introduction

The mammalian vertebral column comprises successive units organised into five series that are highly conserved and easily recognised: cervical, thoracic, lumbar, sacral and caudal. Cervical vertebrae are traditionally distinguished from thoracic vertebrae by the absence of movable rib articulations. The number of cervical vertebrae has remained constant at seven for at least 200 million years, despite variable counts in other regions of the mammalian vertebral column and in the cervical vertebrae of other vertebrate classes (Crompton and Jenkins 1973; Galis 1999; Narita and Kuratani 2005). The diversity of neck length and shape in mammals has evolved under the rigorous constraint of cervical number (Narita and Kuratani 2005). The long neck of giraffes also follows the cervical constraint; therefore, each cervical vertebra is prominently longer than that of the common short-necked ruminants, including okapi (Badlangana et al. 2009; van Sittert et al. 2010).

A previous study raised the possibility that giraffes had gained an additional rib-bearing cervical vertebra in association with their neck elongation (Solounias 1999). Skeletal comparisons between giraffe and okapi revealed morphological transformations of the vertebrae between the seventh cervical vertebra (C7) and second thoracic vertebra (T2) in giraffe. The most notable transformation is observed at C7. In okapi, C7 is obviously differentiated from other cervical vertebrae by its exhibition of an elongated neural spine and lack of the transverse foramen and ventral tubercles (Fig. 4-1c, d). Conversely, C7 in giraffe presents the characteristics that are generally observed between C3 and C6: it contains the transverse foramen, ventral tubercles, short neural spine and

elongation of vertebral body (Fig. 4-1a, b; Lankester 1908; Solounias 1999; Danowitz and Solounias 2015). In case of giraffes, various morphological features generally observed in C7 are found in T1 (Fig. 4-2). For example, the vertebral length of T1 of giraffe represents an intermediate value between the cervical and other thoracic vertebrae (Solounias 1999; Badlangana et al. 2009). The facet type of vertebral articulation is transitional from the radial type to the tangential type at the joint between T1 and T2 in giraffe, whereas the transitional point of articulation lies between C7 and T1 in okapi, which represents the typical ruminant pattern (Fig. 4-3; Lankester 1908; Solounias 1999). Additionally, the configuration of roots of the brachial plexus supports the structural similarity between T1 of giraffe and C7 of okapi (Solounias 1999). From the osteological and neurological evidences, previous studies have proposed the idea that T1 of giraffe is homologous with C7 of okapi (Lankester 1908; Solounias 1999).

Despite many morphological similarities between T1 of giraffe and C7 of okapi, prior studies have criticised the idea of a rib-bearing cervical vertebra in giraffe by the presence of the movable rib in T1: a conclusive criterion for classifying a vertebra as a thoracic vertebra (Mitchell and Skinner 2003; Badlangana et al. 2009; Endo et al. 2009; van Sittert et al. 2010). Additionally, the ribs articulating to T1 connects to the sternum. Therefore, T1 of giraffe has been regarded as merely one of thoracic vertebrae, and the functional insight of this transformation of the vertebral shape has not been mentioned. Revealing the specific function of these modified vertebrae will allow us to understand the evolutionary and ethological advantages of the morphological transformations of the vertebrae in giraffe. Given the general linkage between the vertebral shape and mobility

in vertebrates (Slijper 1946; Townsend et al. 1983; Townsend and Leach 1984; Milne 1991; Long et al. 1997; Stevens and Parrish 1999; Boszyk et al. 2001; Buchholtz 2001; Stevens 2002; Buchholtz and Schur 2004; Taylor et al. 2009; Kuznetsov and Tereschenko 2010; Stevens 2013; Granatosky et al. 2014), morphological similarities imply that T1 of giraffe bears a kinematic resemblance to C7 of okapi. The C6/C7 and C7/T1 joints are highly specialised, facilitating the ventral flexion of the head–neck complex in quadrupedal mammals (Graf et al. 1995); hence, I can presume that giraffe may have gained an additional movable joint contributing to the ventral flexion of neck into the T1/T2 joint. Here I evaluated the ability of the ventral flexion of vertebrae around the cervicothoracic area in giraffe and described the musculoskeletal structure of the neck to reveal a functional significance of the morphological shift of the vertebral column.

Materials and Methods

Analyses of sagittal mobility of each vertebra

For evaluating the mobility of each vertebral joint, I conducted the flexion experiment using giraffe and okapi carcasses. I forcibly moved their neck from the maximum ventral flexion posture to the maximum upraised posture, and recorded the positional relationship of each vertebra in both postures by using the photography and computed tomography. I calculated the angle of a vertebra relative to the posterior adjacent vertebra in the cases of the maximal dorsal and ventral flexion of neck (Fig. 4-4). The angle between two adjacent vertebrae was measured with reference to the line connecting the anterior edge and posterior edge of the articular process in the vertebrae

(Fig. 4-4b). The motion range of each vertebra in a dorsoventral direction was evaluated by the difference between the angle in the dorsal and ventral flexion. In one giraffe and okapi, the angle was calculated from three-dimensional data obtained by computed tomographic imaging. I constructed the three-dimensional model from the computed tomography images by using the Osirix Imaging Software (version 6.5.2; <http://www.osirix-viewer.com/ContributionOsiriX.html>), and then measured the mobility of each vertebral joint. In the other giraffe, I removed some epaxial muscles located on one side to observe the positional relationships of the articular processes, which were then photographed from a lateral view in both postures (Fig. 4-4a). In this study, I measured the motion range of the two most caudal cervical and first five thoracic vertebrae.

Description of musculoskeletal structure

I described the morphological relationships between the thoracic vertebrae and ribs in giraffe and okapi to reveal the osteological restriction on intervertebral flexion movement imposed by ribs. The costovertebral joints were observed using dried skeletons of giraffe and okapi. For inferring the effect of rib articulation against vertebral movement, I described the positions of costal foveae on thoracic vertebrae and the positional relationships between two adjacent vertebrae and a rib.

I dissected giraffe and okapi carcasses and then described the muscular system generating the force resulting in the ventral flexion of the vertebrae for inferring the active ability of the vertebral flexion of giraffe. Gross anatomical dissections of giraffe and okapi were conducted sequentially from the superficial to the deep layer (Fig. 4-5).

Specimens were fresh-frozen and thawed before dissection. I focused on *Musculus longus colli*, located on the ventral surface of the vertebral body, that is the main muscle responsible for ventral flexion of the neck (Smuts and Bezuidenhout 1987). Previous studies about the anatomy of giraffe have noted that *M. longus colli* represents a normal structure in giraffe; however, they reported only the structure of the cervical part of the muscle without addressing the muscular structure around the cervicothoracic area displaying the particular morphological transformations of the vertebrae (Owen 1839; Murie 1872). Solounias (1999) mentioned differences in the attachment area of the muscle between giraffe and okapi, although the muscular structure was not reported in detail. I described the origins and insertions of the muscle in giraffe and okapi, following which the active mechanism of lowering their head and neck was discussed.

The terminology of the vertebrae and muscles was consistent with the prior works of the vertebral column of Giraffidae (Solounias 1999; Danowitz and Solounias 2015).

Specimens

In the flexion experiment, I utilised the carcasses of two giraffes and one okapi, with all being former zoo animals. All were new-born specimens of a few days old, possessing the intact axial skeleton because infant specimens allow easier conduct of the flexion experiment. The skeletal structure around the cervicothoracic area was described by observing dried skeletons of eight adult giraffes and five okapis. Data of the muscular structure was obtained from the carcasses of six giraffes and one okapi. Individual

information regarding the specimens used in this study is listed in Table 4-1.

Results

Estimated sagittal mobility of each vertebra

The flexion experiment revealed that the motion range of each vertebra gradually declined through three successive vertebrae at the cervicothoracic area and that the pattern of decline was different between giraffe and okapi (Fig. 4-6). In giraffe, the estimated ranges of motion were clearly large in C6 and C7 and decreased progressively in the caudal direction from C7 to T2. T1 of giraffe exhibited an intermediate motion range between C7 and T2 and possessed a greater mobility than the remaining thoracic vertebrae. The motion range of each vertebra maintained a low value between T2 and T5 (Fig. 4-6). Conversely, in okapi, the reduction of the motion range was confirmed between C6 and T1. The motion range of C7 showed an intermediate value between C6 and T1, and the ranges of the vertebrae between T1 and T5 represented a low mobility. The results showed that the decreasing point of the vertebral mobility was shifted posteriorly in giraffe, and that the intermediate mobility was observed in T1 of giraffe and C7 of okapi. This indicates the possibility that giraffes have acquired an additional movable articulation into the T1/T2 joint and that the kinematic characteristic of T1 of giraffe is similar to C7 of okapi in the dorsoventral movement of the neck.

Skeletal structure

All thoracic vertebrae of giraffe and okapi, with exception of T1 of giraffe,

possessed three costal foveae at a lateral surface of each vertebra: cranial costal fovea, caudal costal fovea and costal fovea of the transverse process. The cranial costal fovea was located on the lateral side of the outer border of the cranial convex extremity of the vertebral body, and the caudal costal fovea was positioned on the exterior edge of the caudal concave extremity of the vertebral body. However, the cranial and caudal costal foveae in T1 of giraffe were not confirmed. T1 possessed an isolated costal fovea located on the central area of the lateral side of the vertebral body below the transverse process.

According to the skeletal observations, the capitulum of the first rib in giraffe made contact with the isolated fovea and did not touch the caudal part of the vertebral body of C7 (Fig. 4-7a). The second rib articulated with T2 at the cranial costal fovea and costal fovea of the transverse process, without contacting the vertebral body of T1 (Fig. 4-7b). In the third rib, the capitulum of the rib was jointed to the socket formed by the caudal costal fovea of T2 and the cranial costal fovea of T3, and the tuberculum of the rib was attached to the costal fovea of the transverse process of T3 (Fig. 4-7c). For ribs positioned more caudal than the third rib, the costovertebral joints represented the same articulation system as that of the third rib. Namely, in giraffe, thoracic vertebrae typically possess ribs at the cranial and caudal joints of one vertebra, but T1 of giraffe has ribs only at the central area of the lateral side of the vertebral body without disturbing both joints of the vertebra.

In okapi, the costovertebral joint between the first rib and T1 displayed a structural similarity to the joint between the second rib and T2 in giraffe: the capitulum of the rib was attached at the cranial costal fovea of T1 without touching the caudal edge

of the vertebral body of C7 (Fig. 4-8a). In all ribs except the first, the capitulum of the rib was jointed to the socket formed by the caudal and cranial costal foveae of the two adjacent vertebrae, and the tuberculum of the rib articulated with the costal fovea of the transverse process (Fig. 4-8b, c). Thus, the thoracic vertebrae of okapi, including T1, generally possessed the ribs on the cranial and caudal joints of the vertebral body.

Muscular structure

In giraffe, the *M. longus colli* consisted of several incompletely fused segments covering the ventral aspect of vertebral bodies of cervical and thoracic vertebrae from atlas to T7, and was divided into cervical and thoracic parts (Fig. 4-9). The cervical part arose on the concave ventral surfaces from C2 to T2 and was composed of six incompletely separated segments. The five cranial segments originated from the ventral edge of the ventral tubercles between C3 and C7, were directed craniomedially and partially terminated on the ventral spine of two preceding vertebrae by tendinous fibres. The most caudal and deepest segment arose from the hypapophysial tubercles of T1 and T2, following a parallel course on the ventral surface between C7 and T2. The thoracic part comprised two segments that were partly fused. The medial part of it arose from the hypapophysial tubercles between T2 and T4, and inserted on the caudal edge of the dorsal tubercle of C6 as a tendon. The lateral part originated from the convex surfaces between T2 and T7 and terminated on the dorsal tubercle of C7 as a tendon. The muscle attached to the ventrolateral surface of the vertebral body of T1 without tendinous origin and insertion.

In okapi, the muscle arose on the ventral surface of the vertebral bodies from the atlas to T6. The cervical part attached on all cervical vertebrae and the first thoracic vertebra, and the thoracic part extended from the six most cranial thoracic vertebrae to C6 (Fig. 4-9). The components of the cervical part were five segments. The four cranial segments were located on the ventral surface from atlas to C5 and were directed craniomedially, and the most caudal segment was distributed on the ventral area between C6 and T1 and ran parallel to the vertebral column. No obvious tendinous insertion was confirmed in C7. The thoracic part of the muscle arose on the ventral surfaces of the vertebral bodies from T1 to T6 and terminated on the caudal edge of the ventral lamella of C6 as two tendinous fasciculi. This muscle was located on the ventrolateral space of C7 without tendinous origin and insertion. A comparison of the muscular structure of giraffe and okapi revealed that the attachment area of *M. longus colli* in giraffe was expanded posteriorly from T1 to T2 in the cervical part and that the origin and insertion of the muscle were partly shifted posteriorly in the thoracic part (Fig. 4-9).

Discussion

Behavioural advantages of the additional movable vertebra in the giraffe neck

A long neck has evolved independently in various taxa and consequently plays an important role in expanding the reachable space during foraging, improving the predator detection and displaying dominance in competing males (Taylor et al. 2009; Wilkinson and Ruxton 2012). The long neck of the giraffe is the most famous example for understanding the evolution of neck elongation. Its neck has been considered to have

evolved as a result of the adaptive evolution to high browsing behaviour and/or combat behaviour between males (Simmons and Scheepers 1996; Cameron and du Toit 2007; Simmons and Altwegg 2010). The height of the head would significantly influence their fitness. In giraffe, the maximum reachable height of the head is elevated by their long necks and limbs (Pincher 1949). The forelimbs of giraffe are longer than the hind limbs; therefore, their trunk slopes from the cranial to the caudal direction, although the common ruminants, including okapi, show a horizontal trunk (Colbert 1938; Mitchell and Skinner 2003). The pronounced slope of the trunk in giraffe facilitates elevating the position of the cervicothoracic transition of the axial skeleton, resulting in a rise of the entire neck. The adaptive modifications of the body plan of giraffe pose difficulties when lowering the head to the ground surface level for drinking water (Pincher 1949). As a consequence, the development of a method of lowering the head and neck to facilitate the extension of the dorsoventral reachable space of the head was necessitated.

The flexibility of the axial skeleton is generally determined by two variables: the total number of movable vertebrae and the maximum mobility of each vertebral joint (Brainerd and Patek 1998; Preuschoft and Klein 2013). The mammalian thoracic region is rigid to facilitate respiration during locomotion and to counteract loading forces transmitted from the limbs (Schilling and Hackert 2006; Filler 2007). Previous studies assumed that the majority of the head and neck movement occurred in the cervical region (Jeffcott 1979; Selbie et al. 1993; Stevens and Parrish 1999; Taylor et al. 2009), suggesting that the total number of movable vertebrae is at a constant seven in the mammalian neck. Nevertheless, the present study proved the expansion of the motion

range in C7 of giraffe and the mobility acquisition in T1 of giraffe (Fig. 4-6).

The head and neck of mammals are considered collectively as a loaded beam that is supported at one end only by attachment to the cranial end of the trunk region (Slijper 1946). The cervical spine is regarded as an extended third-class lever: the resistance occurs on one side of an effort force, whereas the fulcrum is located on the other side (Davidovits 2007). The present study suggests that the T1/T2 joint complex in giraffe acts as a fulcrum in this system. Conversely, the C7/T1 joint complex works as a fulcrum in okapi. It is predicted that a small increment of the dorsoventral mobility in the C7/T1 and T1/T2 joints in giraffe would result in a large displacement at cranial end level of the cervical spine, owing to their extraordinarily long neck.

Kinematic characteristics of C7 and T1 in giraffe

The articulation of the rib is a principal factor restricting intervertebral flexion (Filler 2007). The rib typically articulates with the vertebrae through two positions in mammals: the costal fovea of the transverse process and the socket formed by the caudal and cranial costal foveae of two adjacent vertebrae (Liebich and König 2006). This pattern was confirmed in the rib articulations in giraffe and okapi. It imposes a fixed distance between the caudal costal fovea of a vertebra and the transverse fovea of the posterior adjacent vertebra, thereby creates a strict limitation on vertebral flexion (Filler 2007). However, in giraffe, the capitula of the first and second ribs did not make contact with the vertebral bodies of the adjacent vertebrae; consequently, in this region, the immobilisation distance resulting from the rib articulation did not affect the vertebral

flexion at C7/T1 and T1/T2 joints, suggesting that the change of articular positions of the capitula of ribs in giraffe might minimise the restriction of vertebral mobility imposed by ribs around T1.

The attachment area of *M. longus colli* in giraffe demonstrates that the rotational force generated by the thoracic part of this muscle tends to be concentrated to their C6 and C7 by the strong tendons (Fig. 4-10). Although the force might act on T1, it would be lower than the power exerted in C6 and C7 due to the absence of the tendinous insertion in T1 of giraffe. Conversely, in okapi, the muscle would work more intensively on C6 than on C7, since C7 does not possess tendinous insertion (Fig. 4-10). T1 of okapi does not possess the insertion; therefore, the muscle does not produce the rotational force on the vertebra. The vertebral movement inferred by the muscular structure is consistent with the result of the flexion experiment.

According to previous osteological studies, C7 of giraffe possesses a long vertebral body, a round articular surface at the caudal joint between the vertebral bodies and large articular facets directed laterally on the posterior articular processes (Table 4-2) (Lankester 1908; Solounias 1999; Badlangana et al. 2009; van Sittert et al. 2010). These characteristics are generally observed in the vertebrae from C2 to C6 and could be regarded as the features representing high intervertebral flexibility, based on prior studies on the relationships between the vertebral shape and mobility (Stevens and Parrish 1999; Boszyk et al. 2001; Buchholtz and Schur 2004; Kuznetsov and Tereschenko 2010; Stevens 2013). The thoracic vertebrae from T2 to T14 display the vertebral shape representing low intervertebral mobility (Stevens and Parrish 1999; Boszyk et al. 2001;

Buchholtz and Schur 2004; Kuznetsov and Tereschenko 2010; Stevens 2013). Namely, these vertebrae represent a short vertebral length, a flat articular surface at the caudal joint of the vertebral body, a long neural spine and small articular facets directed medially just beneath the neural spine with no processes (Table 4-2) (Lankester 1908; Solounias 1999). Additionally, T1 of giraffe represents the intermediate characteristics between the general cervical and thoracic vertebrae (Lankester 1908; Solounias 1999). The vertebral body of T1 in giraffe is slightly longer than the other thoracic vertebrae and shows an intermediate length between the cervical and thoracic vertebrae (Badlangana et al. 2009). T1 possesses two paired, large articular facets on the small posterior articular processes beneath the neural spine (Lankester 1908). The vertebra presents a flat articular surface of the vertebral body on the joint between T1 and T2. The long vertebral body, the large articular facets, and the posterior articular process would contribute to facilitating a higher vertebral mobility than that of general thoracic vertebrae (Boszczyk et al. 2001; Buchholtz and Schur 2004; Kuznetsov and Tereschenko 2010; Stevens 2013); however, the flat articular surface of the vertebral body would enhance the rigidity between the joints (Buchholts and Schur 2004). This suggests that T1 of giraffe potentially possesses an intermediate mobility between the general cervical and thoracic vertebrae.

Conversely, T1 of okapi possesses the same vertebral shape as the remaining thoracic vertebrae, representing low vertebral mobility (Solounias 1999). In okapi, the intermediate shape is confirmed in C7 (Solounias 1999), suggesting that C7 of okapi presents lower mobility than the remaining cervical vertebrae. The vertebral morphology corresponds with the results regarding the expansion and acquisition of the vertebral

flexibility in the C7/T1 and T1/T2 joints in giraffe.

Solounias (1999) hypothesized that the vertebra traditionally identified as T1 might be actually regarded as 'the eighth cervical vertebra' based on specific anatomical characteristics of the general cervical vertebrae; however, the first thoracic vertebra has been overlooked as merely one of thoracic vertebrae since it possesses the movable ribs. The present study provided anatomical evidences that T1 of giraffe played a kinematic role corresponding to the C7 of general ruminants even if the vertebra articulated with the sternum via the movable ribs. Note that, in this study, there is no evidence supporting that a cervical vertebra is added between C3 and C6, and that T1 is originally cervical vertebra. The results indicate that the morphological shift of the vertebrae of giraffe at cervicothoracic area has great significance in understanding evolutionary functional plasticity of the mammalian vertebral column rather than in discussing the number of cervical vertebrae.

Developmental background of the morphological shift of the vertebral column

The musculoskeletal structure of the axial skeleton consists of two elements derived from different developmental backgrounds: primaxial and abaxial elements (Burke and Nowicki 2003; Nowicki et al. 2003; Wellik 2007; Durland et al. 2008). The vertebrae, vertebral ribs and epaxial and hypaxial muscles develop only from somitic mesoderm and are classified as the primaxial elements. The sternum and limbs originate from lateral plate mesoderm and are identified as the abaxial elements (Fig. 4-11; Burke and Nowicki 2003). The abaxial domain contains somitic cells that migrate into the lateral

plate environment early during development and mix with lateral plate cells (Burke and Nowicki 2003). Curiously, in mice, the first rib is completely identified as an abaxial element (Durland et al. 2008). The expression patterns of *Hox* genes, regulating the morphology of the vertebral column and rib cage (Burke et al. 1995; Johnson and O'Higgins 1996; Wellik and Cappecci 2003; McIntyre et al. 2007; Wellik 2007; Vinagre et al. 2010), are independent between the primaxial and abaxial domains (Nowicki and Burke 2000; Burke and Nowicki 2003; McIntyre et al. 2007). In the abaxial domain, the migrating somitic cells adopt the *Hox* expression of the lateral plate mesoderm into which they migrate (Burke and Nowicki 2001). Additionally, a primaxial patterning possesses a colinearity of the phenotype, whereas an abaxial patterning is not colinear (McIntyre et al. 2007). Colinearity is the phenomenon that the order of the *Hox* genes along the chromosome corresponds with the order of the expression domains of the genes along the anterior-posterior axis of the embryo. Mutations of the *Hox* genes cause the homeotic transformation in primaxial elements, whereas it results in serious patterning defects in the abaxial elements (Jeannotte et al. 1993; Kostic and Cappecci 1994; Rancourt et al. 1995; McIntyre et al. 2007).

In the light of the above evidence obtained from previous genetic studies, I considered the possibility that the mutations of *Hox5* and/or *Hox6* specific to the primaxial domain would have resulted in the transformations of the musculoskeletal structure in the neck of giraffe. Both genes are important for the specification of the identity of the vertebral column between C6 and T1 (Medina-Martínez et al. 2000). *Hox6* genes function to induce ribs by regulating *Myf5/Myf6* expression, suggesting that their

expression pattern is responsible primarily for the regionalisation of the vertebral column between the cervical and thoracic vertebrae (Vinagre et al. 2010). When I consider the genetic background of the development of the vertebrae and ribs in giraffe along with the evidence obtained from mice, it could be assumed that the mutations of the *Hox5* and/or *Hox6* genes specific to the primaxial domain caused the morphological transformations of the vertebrae and ribs, with the exception of the first rib. From the study of mice, it has been predicted that the development of the first rib would be regulated by the *Hox* expression pattern in the abaxial domain (Durland et al. 2008), indicating that the phenotype of the first rib is unaffected by the mutations of the *Hox* genes specific to the primaxial domain. Therefore, it could now be explained that the mutations of the *Hox* genes specific to the primaxial domain causes the morphological transformations of the vertebrae in giraffe without displacing the position of the rib cage.

Conclusion

I quantitatively demonstrated the expansions of the motion range in C7 and T1 of giraffe by the flexion experiment. The muscular system generating a vertebral rotation was partly modified around the cervicothoracic region, which supported the result of the estimation of the vertebral mobility. The modifications of the attachment position of the capitula of the first and second ribs in giraffe minimise the restriction on vertebral flexion imposed by ribs, thereby enabling notable flexion of the joint between T1 and T2. The addition of movable articulation to the thoracic region results in a large displacement of the head, even if the mobility is relatively smaller than that of the cervical joints. Based

on my findings, I assert the evolutionary importance of the increased mobility at the base of the neck in terms of the advanced adaptation to high browsing in giraffe. Provided that the total neck length of adult giraffe is 2 m, the additional mobility at T1/T2 joint expands a reachable space of head and neck by about 50 cm (Fig. 4-12). Under the rigorous cervical constraint, giraffe have achieved the functional novelties at the cervicothoracic region by subtle modifications in their existing musculoskeletal system.

Recent studies have reconsidered the regionalisation of the vertebral column by focusing not on the presence of movable ribs but on the morphological characteristics of the vertebrae (Buchholtz and Stepien 2009; Hautier et al. 2010; Head and Polly 2015). Tree sloths are well known to exhibit an abnormal number of cervical vertebrae: *Bradypus* (three-toed sloths) possess eight to ten cervical vertebrae, whereas *Choloepus* (two-toed sloths) possess five to eight cervical vertebrae (Buchholtz and Stepien 2009). However, the morphological characteristics and the ossification pattern of the vertebrae have demonstrated that the boundary between the cervical and thoracic region was identified between seventh and eighth vertebrae, as is the case in other mammals (Bell 1833; Buchholtz and Stepien 2009; Hautier et al. 2010). These studies regarded the abnormal number of cervical vertebrae in sloths as rib-less thoracic vertebrae in the neck or rib-bearing cervical vertebrae in the thorax (Hautier et al. 2010). They proposed the idea that the constraint of the cervical vertebrae was actually conserved even in the sloths that had historically been the most famous group thought to deviate from the constraint (Buchholtz and Stepien 2009). This idea offered new insight, clearly different from the previous perception, into the regionalisation of the vertebral column in mammals. The findings in

this study additionally provide evidence that the vertebral regionalisation in giraffe is slightly shifted posteriorly at the cervicothoracic transitional region without changing the traditional border based on the presence of movable ribs. This suggests the possibility that the vertebral regionalisation is additionally diversified in other mammals that maintain the normal number of cervical vertebrae. I advocate that subtle mutations of the *Hox* genes can induce the striking structural and functional novelties in the conservative existing system.

Table 4-1 Materials used in this study.

	Species	Specimen	Age	Sex	Flexion experiment	Skeletal observation	Dissection	Donor
Giraffe	<i>Giraffa camelopardalis</i>	UMUT-09147	8-year-old	Male		*		Kobe Oji Zoo
		UMUT-10071	15-year-old	Female		*		Hamamatsu Zoological Garden
		UMUT-10072	21-year-old	Male		*		Hamamatsu Zoological Garden
		UMUT-13037	19-year-old	Male		*	*	Hirakawa Zoological Park
		UMUT-13055	8-year-old	Male		*	*	Kobe Oji Zoo
		UMUT-13056	5-year-old	Male		*	*	Chiba Zoological Park
		UMUT-14140	Adult	Male		*		No information
		UMUT-15052	11-year-old	Male		*	*	Toyama Municipal Family Park
		NSMT-M43076	Newborn	Female	*		*	Tama Zoological Park
		NSMT-M43180	Newborn	Male	*		*	Tama Zoological Park
Okapi	<i>Okapia johnstoni</i>	KPM-NF1005125	Newborn	Male	*		*	Zoorasia Yokohama Zoological Gardens
		NSMT-M-35837	11-year-old	Female		*		Ueno Zoological Gardens
		MNHN-ZM-AC-1959-262	Infant	Female		*		No information
		MNHN-ZM-AC-1968-119	Adult	Female		*		No information
		MNHN-ZM-AC-1975-101	Adult	Male		*		No information
		MNHN-ZM-AC-1990-43	Adult	Male		*		No information

Asterisks means the specimen used in each work. We conducted the macroscopic dissection in UMUT-13037, 13055, 13056, 15052, and observed the skeletal structure after making the skeletal specimens in these materials.

Table 4-2 Morphological characteristics of a vertebra in relation to the mobility at cervicothoracic area in giraffe and okapi.

Characteristics	Giraffe				
	C2-C6	C7	T1	T2	T3
Length of vertebral body ^[1,2]	Long	Long	Intermediate	Short	Short
Articular surface at caudal joint ^[1]	Round	Round	Flat	Flat	Flat
Articular type of vertebral articulation ^[3,4]	By process	By process	By small process	By surface	By surface
Facet type of vertebral articulation ^[4,5]	Radial	Radial	Radial and Tangential	Tangential	Tangential
Size of posterior articular facet ^[6]	Large	Large	Large	Small	Small
Length of neural spine ^[7]	Short	Short	Intermediate	Long	Long

Characteristics	Okapi				
	C2-C6	C7	T1	T2	T3
Length of vertebral body ^[1,2]	Long	Intermediate	Short	Short	Short
Articular surface at caudal joint ^[1]	Round	Flat	Flat	Flat	Flat
Articular type of vertebral articulation ^[3,4]	By process	By process	By surface	By surface	By surface
Facet type of vertebral articulation ^[4,5]	Radial	Radial and Tangential	Tangential	Tangential	Tangential
Size of posterior articular facet ^[6]	Large	Large	Small	Small	Small
Length of neural spine ^[7]	Short	Intermediate	Long	Long	Long

Dark gray area indicates the characteristics relating to the intervertebral stiffness, and the open area shows the characteristics representing the intervertebral flexibility. Light grey area means the intermediate characteristics between them. Morphological characteristics were described in previous studies (Lankester 1908; Solounias 1999; Badlangana et al. 2009; van Sittert et al. 2010; Danowitz and Solounias 2015). Kinematic interpretation of the vertebral morphology is compliant with prior works; 1, Buchholtz and Schur 2004; 2, Stevens 2013; 3, Boszczyk et al. 2001; 4, Kuznetsov and Tereschenko 2010; 5, Milne 1991; 6, Stevens and Parrish 1999; 7, Long et al. 1997.

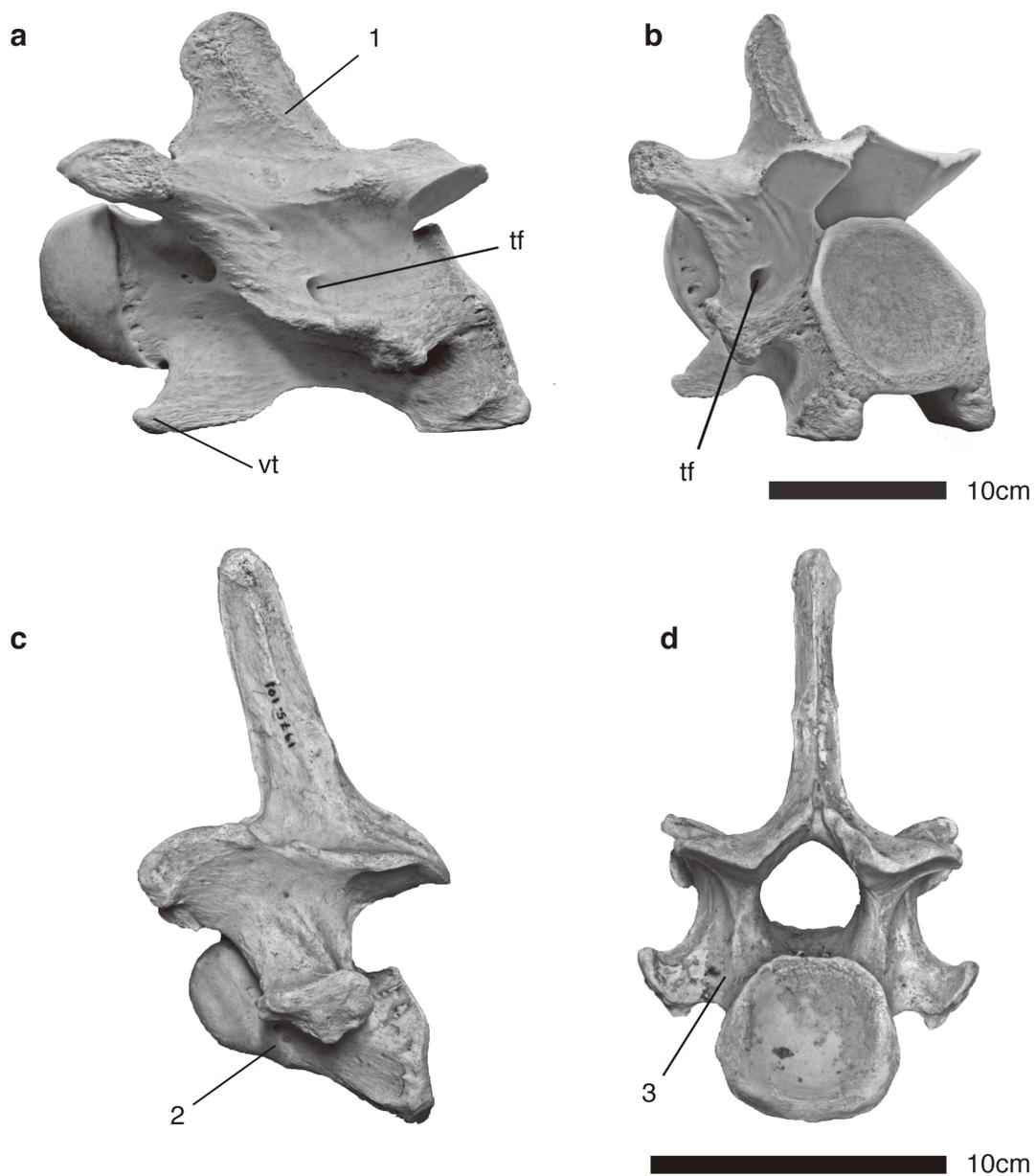


Fig. 4-1 Morphology of the C7 in the giraffe (a, b) and okapi (c, d). (a) The lateral view of the C7 of giraffe. (b) The laterocaudal view of the C7 of giraffe. (c) The lateral view of the C7 of okapi. (d) The caudal view of the C7 of okapi. **tf**, transverse foramen; **vt**, ventral tubercle; **1**, relatively short neural spine; **2**, absence of ventral tubercle; **3**, absence of transverse foramen.

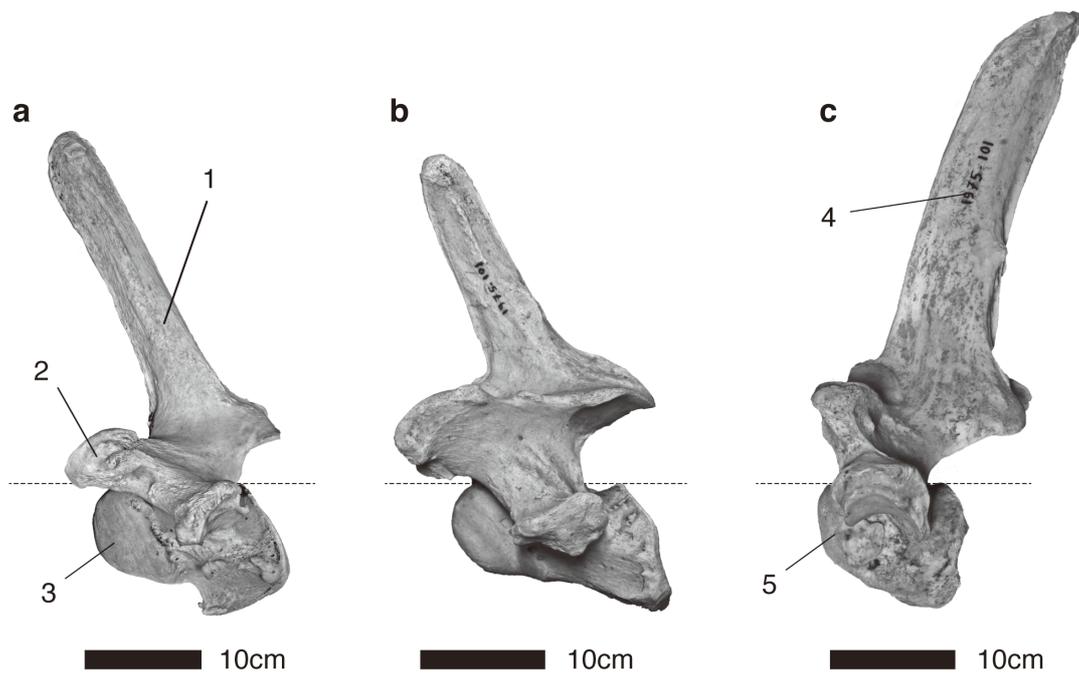


Fig. 4-2 Lateral view of the T1 of giraffe (a), C7 of okapi (b), and T1 of okapi (c). The vertebral angles are adjusted based on the angle of the neural canal. The dashed line means the ventral surface of the neural canal. 1, cranial inclination of the neural spine; 2, large and pillared articular process; 3, round cranial articular surface of the vertebral body; 4, caudal inclination of the neural spine; 5, flat cranial articular surface of the vertebral body.

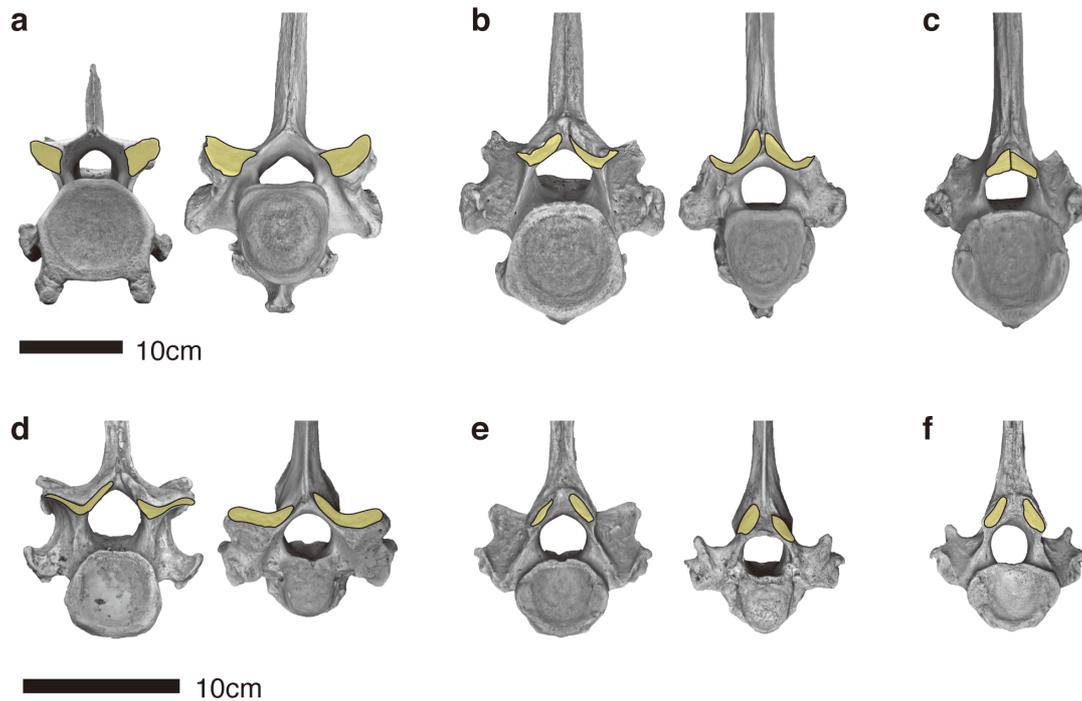


Fig. 4-3 Facet type of vertebral articulation at cervicothoracic area in giraffe (a-c) and okapi (d-f). The region highlighted by yellow indicate the shape of the articular facets in the C7/T1, T1/T2, and T2/T3 joints. (a, d) The articular facets of the C7/T1 joint in giraffe (a) and okapi (d). The posterior facets of the C7 of the giraffe are laterally directed and regarded as the radial type, whereas the facets of the okapi are laterally and medially directed and regarded as the transitional type. (b, e) The articular facets of the T1/T2 joint in giraffe (b) and okapi (e). The posterior facets of the T1 of giraffe are similar to those of the C7 of okapi and regarded as the transitional type. The posterior facets of the T1 of okapi are directed medially and regarded as the tangential type. (c, f) The articular facets of the T2/T3 joint in giraffe (c) and okapi (e). The posterior facets of the T2 are directed medially and regarded as the tangential type both in the giraffe and okapi.

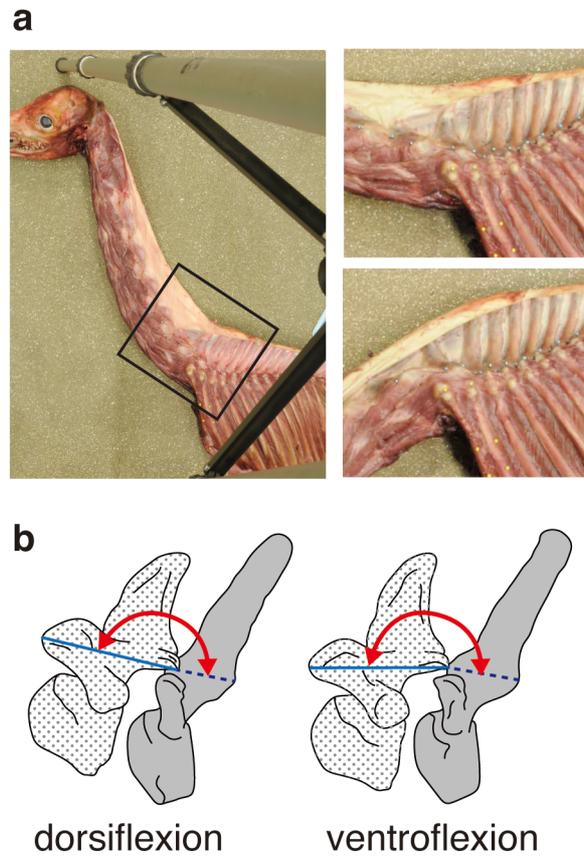


Fig. 4-4 Method of the estimation of motion range of each vertebra. (a) The flexion experiment of the neck using the carcasses of a giraffe. The black square in the left indicates the region in which we analyzed the vertebral mobility. The upper right shows the posture at the moment of the maximal dorsal flexion of the neck, and the lower right displays the posture at the moment of the maximal ventral flexion. (b) The procedure for estimating the vertebral mobility. The motion range of each vertebra was estimated from the angles between adjacent vertebrae both in maximal dorsal (left) and ventral flexion (right). Angles were measured from the lines connecting the anterior and posterior edge of the articular processes and are shown as arc arrows.

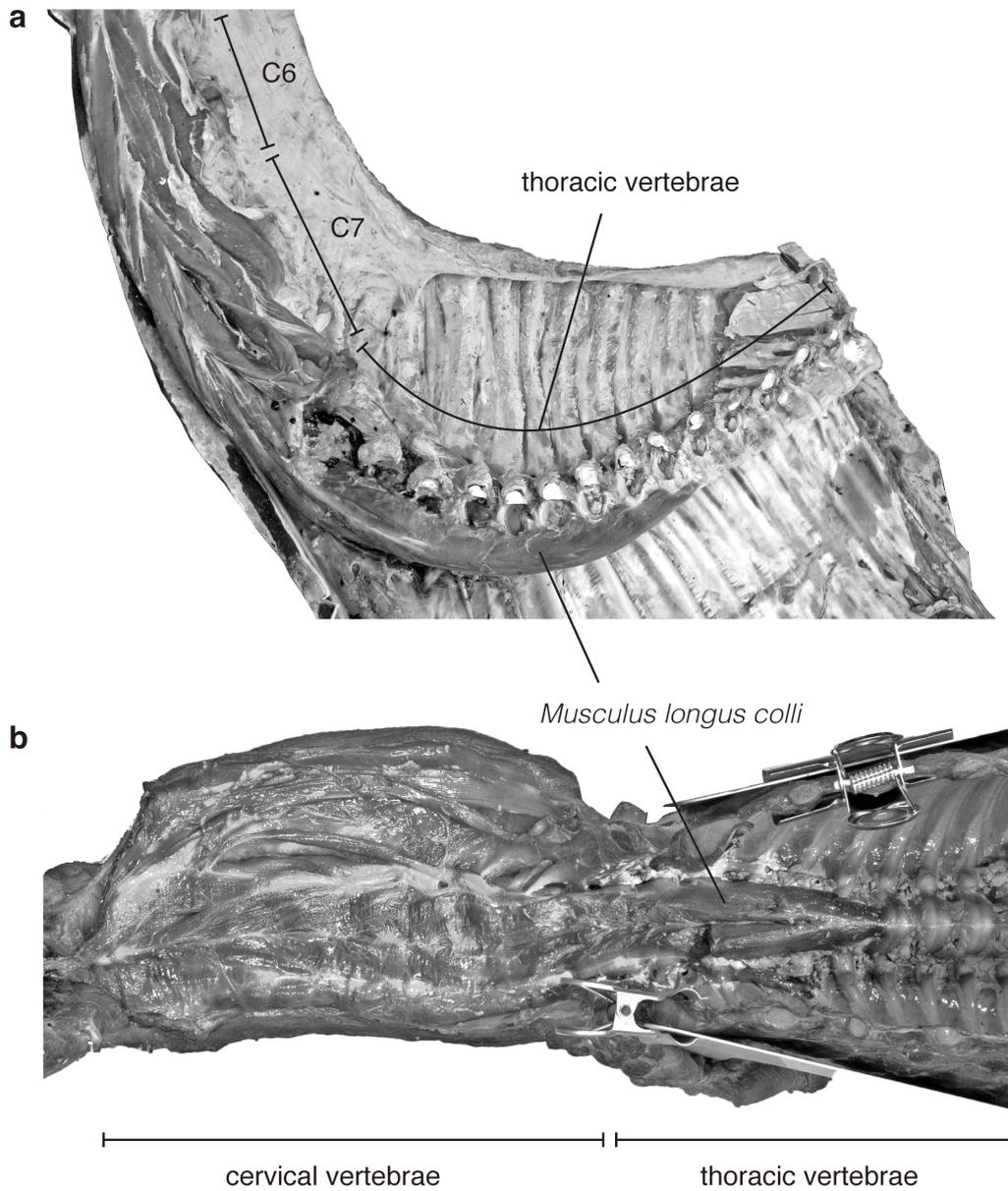


Fig. 4-5 Procedure of gross anatomical dissections. (a) The lateral view of the deep layer of the neck musculature in the giraffe. (b) The ventral view of the deep layer of the neck musculature in the okapi.

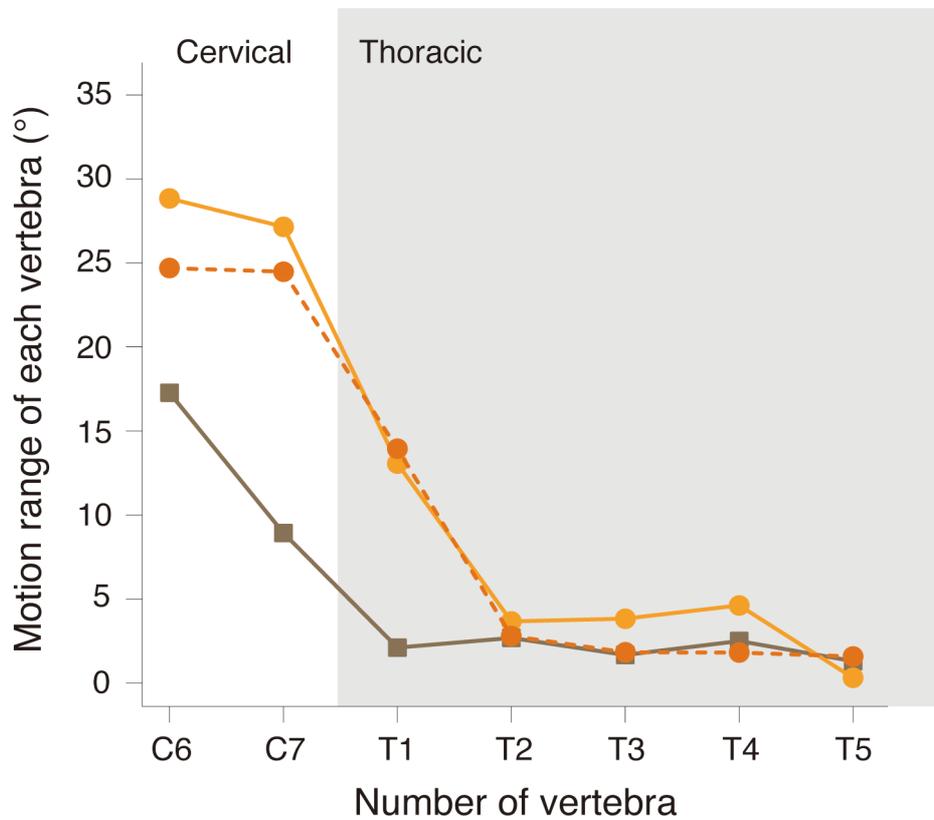


Fig. 4-6 Estimated motion range of each vertebra from C6 to T5 obtained by the flexion experiment. Circles colored by light orange indicate the estimated value of the motion range in a giraffe (NSMT-M43180) and dark orange circles indicate those in the remaining giraffe (NSMT-M43076). Brown squares represent the estimated motion range in okapi (KPM-NF1005125). The shaded area indicates the thoracic region.

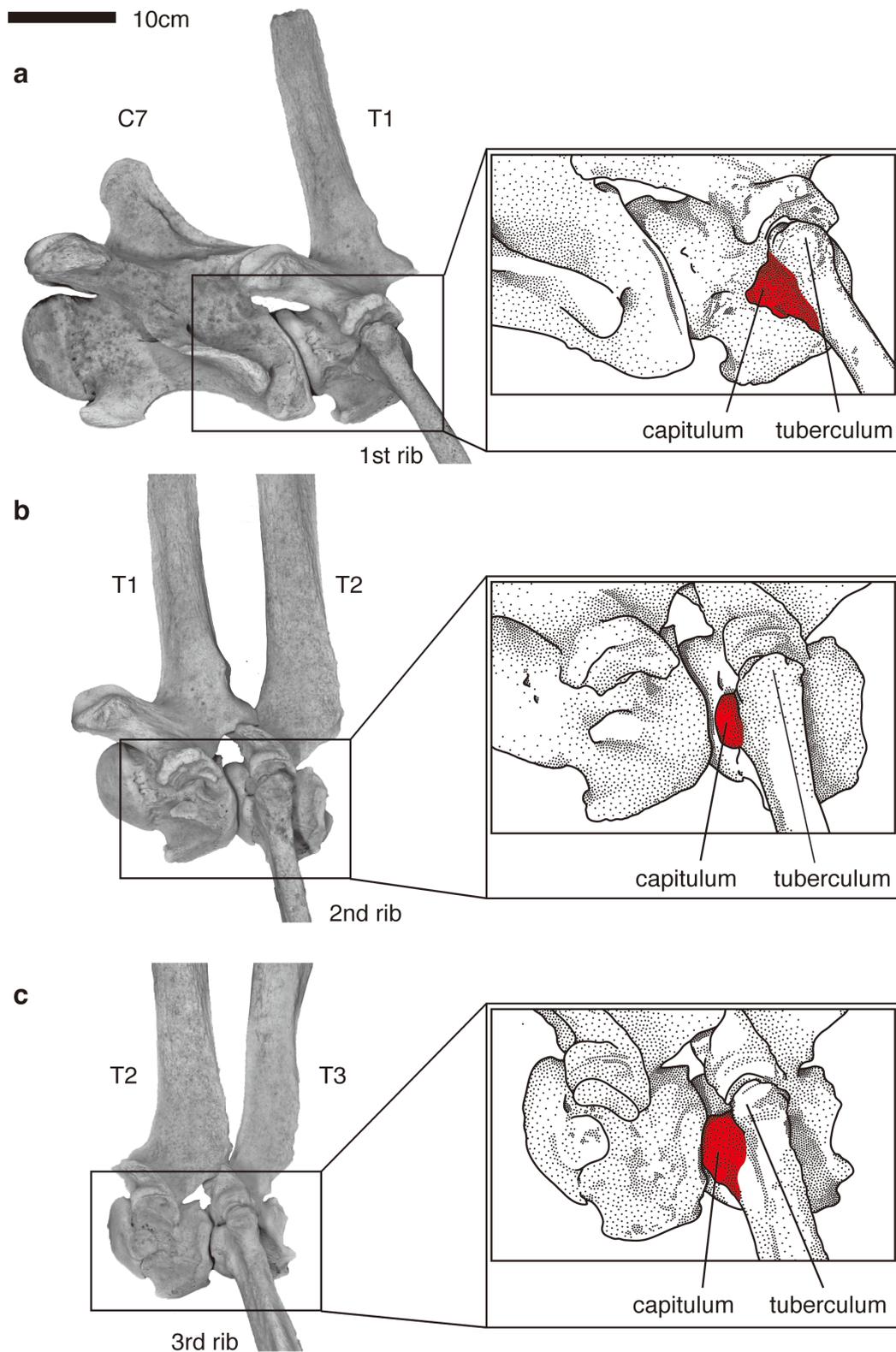


Fig. 4-7 Osteological restriction against vertebral flexion imposed by rib articulation in the giraffe. The first rib attaches on the central area of the lateral surface of T1. The capitulum of the first rib does not connect to the caudal edge of the vertebral body of C7 (a). The second rib articulates with the cranial part of T2. The capitulum of the rib does not disturb the joint between T1 and T2 (b). The capitulum of the third rib is jointed to the socket formed by the caudal costal fovea of T2 and the cranial costal fovea of T3, which restricts the mobility of T2/T3 joint (c). The red area of the ribs indicates the position of the capitulum of the rib. The skeletal specimen is UMUT-13037.

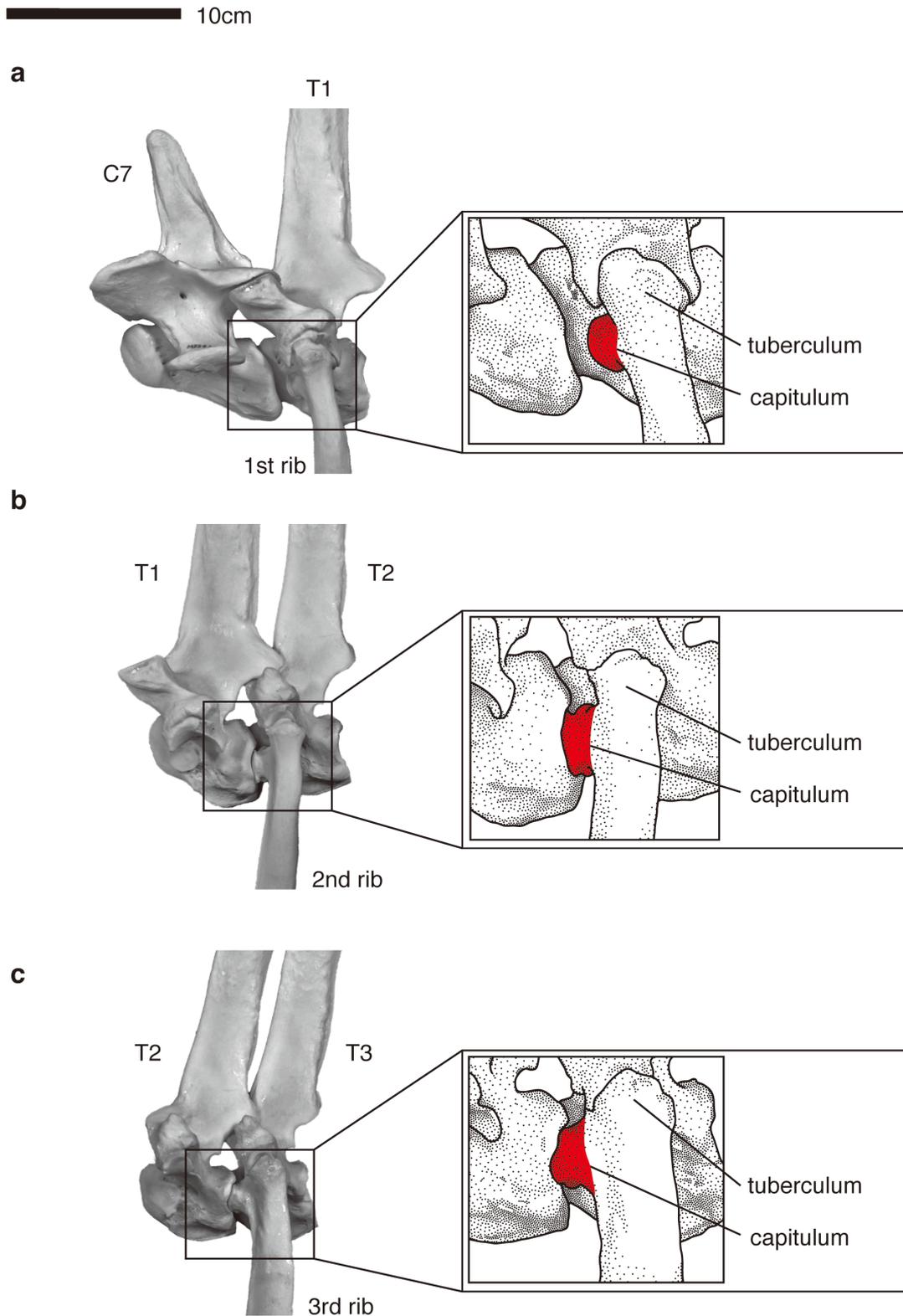


Fig. 4-8 Osteological restriction against vertebral flexion imposed by rib articulation in the okapi. The first rib articulates with the cranial part of T1. The capitulum of the rib does not disturb the joint between C7 and T1 (a). The capitulum of the second rib is jointed to the socket formed by the caudal costal fovea of T1 and the cranial costal fovea of T2, which restricts the mobility of T1/T2 joint (b). The articulation system of the third rib is same to that of the second rib (c). The red area of the ribs indicates the position of the capitulum of the rib. The skeletal specimen is NMNH-1968-119.

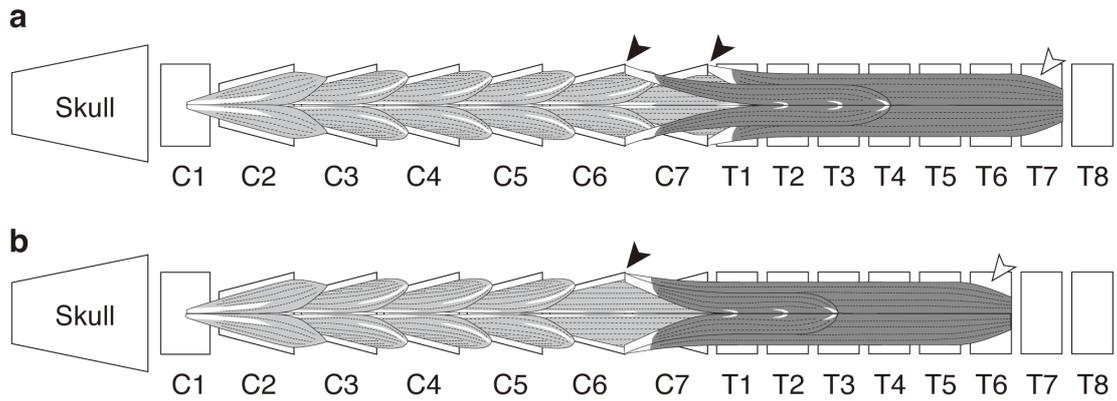


Fig. 4-9 Schematic of muscular structure of *Musculus longus colli* in the giraffe (a) and okapi (b). The diagrammatic illustration colored by light grey indicates the structure of the cervical part of the muscle. The dark grey illustration shows the attachment area of the thoracic part of the muscle. The black arrowheads indicate the tendinous insertion of the thoracic part of the muscle, and the open arrowheads indicate the most caudal attachment area of the muscle.

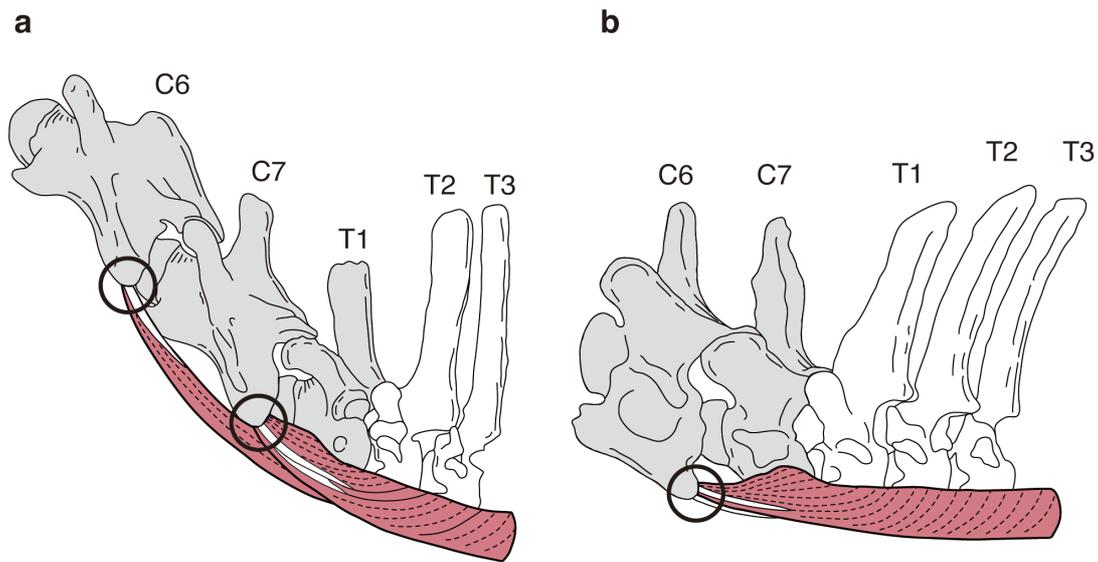


Fig. 4-10 Functional musculoskeletal model of the neck movement at the cervicothoracic area in the giraffe (a) and okapi (b). The vertebrae colored in grey possess the morphological characteristics closely related to high intervertebral flexibility and contain the insertion of the thoracic part of the thoracic part of *Musculus longus colli*. The white vertebrae display the characteristics representing low flexibility and have the origin of the muscle. The illustration of a muscle represents the attachment area of the thoracic part of *Musculus longus colli* and explains the muscular system generating the force to rotate the vertebrae at the cervicothoracic area. The circles indicate the points of the concentration of the force rotating the vertebra generated by the muscle.

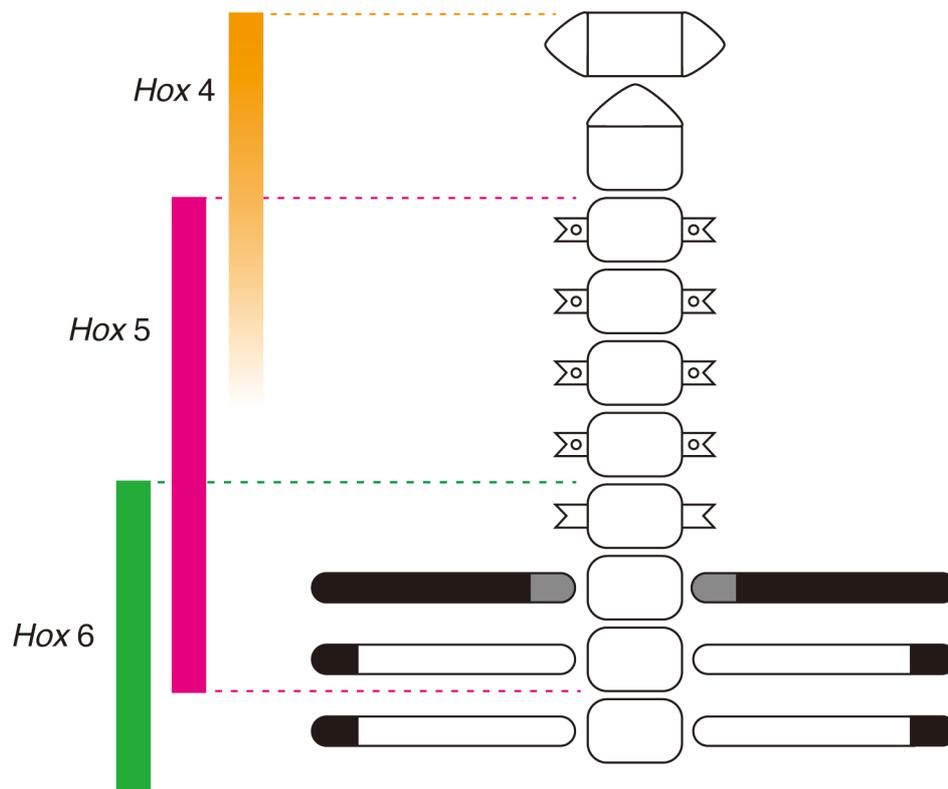


Fig. 4-11 Schematic of the primaxial/abaxial patterning and expression pattern of *Hox* genes in mice. This schematic shows the vertebrae from C1 to T3 and the ribs from first to third. Primaxial structures are represented in white and abaxial structures are represented in black. Shaded structures are of uncertain patterning regime.

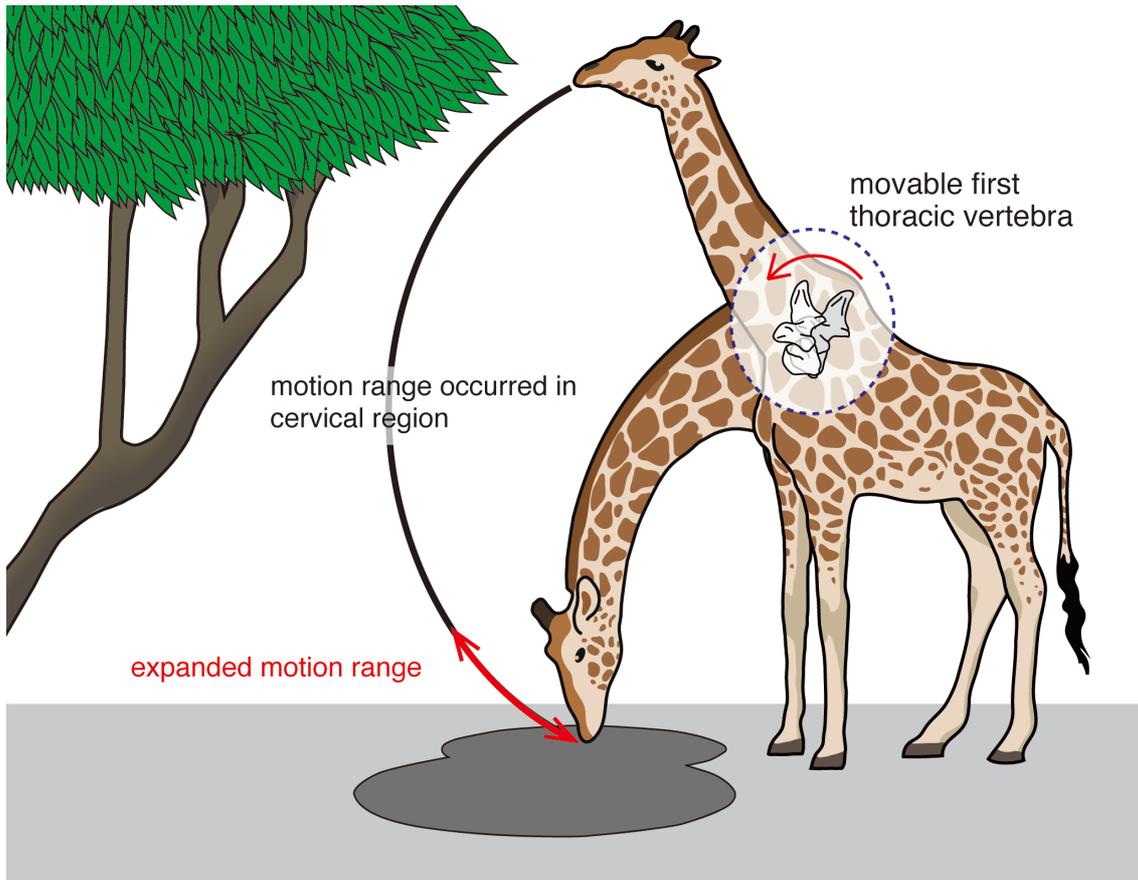


Fig. 4-12 Diagram explaining the ecological advantage of the movable thoracic vertebra of the giraffe. According to our estimation of motion range of T1, the movable T1 contributes to enlarging the reachable space of the head and neck by about 50 cm, and enables eating leaves from treetops and drinking water on the ground. These conflicting requirements are a unique characteristic of the lifestyle in the giraffe.

Chapter 5, Chapter 6 の内容は、学術雑誌論文として出版する計画があるため公表できない。5年以内に出版予定。

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