



Two mammalian species in which the intercostal nerves innervate the serratus anterior or scalenus muscles together with the cervical nerves: an important clue to clarify the homology of cervico-thoracic trunk muscles in mammals

Masahiro Koizumi¹

Received: 4 May 2018 / Accepted: 12 April 2019 / Published online: 24 April 2019
© Japanese Association of Anatomists 2019

Abstract

The levator scapulae, rhomboideus, and serratus anterior muscles (as a group referred to the dorsal shoulder girdle muscles) and the scalenus muscles in mammals are usually innervated by cervical nerves. However, in koalas, the serratus anterior is additionally innervated by the lateral cutaneous branch of the first intercostal nerve. In cats, as in some other mammalian species, a part of the scalenus muscle (scalenus longus muscle) is innervated by the lateral cutaneous branches of the intercostal nerves. A precise comparison of the innervating nerves at the same segment in these two cases could clarify the homological relationship between the cervical and thoracic trunk muscles. In this context, the aim of this study was to follow the nerve fibers included in the nerves supplying the dorsal shoulder girdle and scalenus muscles up to the level of the spinal nerve roots in two koalas and two cats. The resultant observations revealed that both of the nerves to the serratus anterior in koalas and to the scalenus muscles in cats from the lateral cutaneous branch of the intercostal nerve occupy the same position in the spinal roots as the cervical nerve branches to the dorsal shoulder girdle muscles and the thoracic nerve branches to the external intercostal muscle. Based on these results, the axial trunk muscles in the cervico-thoracic region could be classified as follows: the scalenus and dorsal shoulder girdle muscles belong to the same lateral axial trunk muscle group as the external intercostal muscle, and are clearly distinguished from the medial group, such as the internal and innermost intercostal muscle.

Keywords Cat · Comparative anatomy · Koala · Shoulder girdle muscles · Trunk muscles

Introduction

In tetrapods, the axial muscles, which develop from myotomes, can be classified into the epaxial and hypaxial musculatures (Romer and Parsons 1977). Embryological studies have revealed that the ventral trunk and limb muscles, although undergoing a different developmental process, both originate from the same hypaxial musculature group (Buckingham et al. 2003; Francis-West et al. 2003). In mammals, the fundamental segmental arrangement of the ventral trunk muscles has been preserved in the intercostal muscles of the thoracic region. To the contrary, the trunk muscles have lost their segmental structure in the mammalian

cervical region, where the trunk muscles exhibit a greatly modified arrangement in accordance with the absence of a body cavity and the development of the anterior limb. Therefore, when discussing the morphological significance of the cervical trunk muscles, it is important to clarify the homological relationship of the cervical muscles with the intercostal muscles. However, because the cervical and thoracic trunk muscles receive nerves from the different spinal segments, a direct comparison between them is usually difficult. Nonetheless, in some mammals, a direct comparison is possible.

In the study reported here a comparison was made between cats and koalas. In cats, the lower part of the scalenus muscles, which belong to the cervical trunk muscles, is additionally innervated by the thoracic nerves (Crouch 1969). Electrophysiological experiments on cats, which is the animal standardly used in such studies, have clarified the location of motoneuron projecting to the trunk muscles

✉ Masahiro Koizumi
koizumi@tau.ac.jp

¹ Tokyo Ariake University of Medical and Health Sciences,
2-1-9 Ariake, Koto-Ku, Tokyo 135-0063, Japan

(Hörner and Kümmel 1993; Tani et al. 1994; Izumi and Kida 1998). Koalas have been observed because of very important findings on innervations demonstrating homology between the serratus anterior muscle as a cervical trunk muscle and the intercostal muscle as a thoracic trunk muscle. In these cases, the nerves of the same spinal segments were found to innervate both of the cervical and intercostal muscles. These findings can be the important clues to clarify the homological relationship between the cervical and thoracic trunk muscles.

The aim of this study was to determine the precise origins in the cervical and thoracic nerve roots of the branches innervating the dorsal shoulder girdle, scalenus, and intercostal muscles in koalas and cats. The homological relationship between the shoulder girdle and the axial trunk muscles in the cervico-thoracic regions based on these findings is discussed.

Materials and methods

In this study, three sides from two female koalas (*Phascolarctos cinereus*) and two sides from two male cats (*Felis domestica*) were observed (Table 1). Koala no. 2 was donated to the author from Dr. M. Yamasaki (Akita University, Japan, retired). This specimen was originally from the Australian Museum, Sydney, Australia (no. M14074). Both koalas were found dead and then kept frozen at the university or museum facilities. Both cats were obtained after they had been euthanized for earlier studies in brain research at Kumamoto University, Japan (after receiving approval by the institutional animal use committee). No animals were killed for this study. After the specimens were thawed, they were fixed initially in formalin (10%) and then preserved in alcohol (60%) until the start of the study. The first step was to dissect the specimens macroscopically to expose the muscles and nerves of the cervical and upper thoracic regions. The anterior limbs were then removed from the body by cutting each spinal root contributing to the brachial plexus and axillary vessels in order to observe precisely the innervation of the dorsal shoulder girdle and scalenus muscles. In all specimens, with the exception of one of the cats, the dorsal

shoulder girdle muscles and upper intercostal muscles with their nerves and related spinal cords were detached from the bones. To obtain precise observations of the spinal origins of the nerves supplying the dorsal shoulder girdle, scalenus, and intercostal muscles, the nerve fiber compositions were examined by stripping off the epineurium and perineurium, if necessary, under a stereomicroscope.

The protocol for the present study did not include any specific issue that required approval from the Ethics Committee of Tokyo Ariake University. The research described herein conformed to the American Association of Anatomists (AAA's) Guiding Principles in the Care and Use of Animals.

Results

Observations on the brachial plexuses

The brachial plexuses observed in this study were formed by the ventral rami of the lower four (in koalas) or three (in cats) cervical nerves (C5–8 or C6–8, respectively) and the first thoracic nerve (T1). The axillary artery passed through between C7 and C8 in all cases.

Anatomy of the dorsal shoulder girdle and scalenus muscles

The attachments and innervations of each muscle under study in the koala and cat specimens are summarized in Tables 2 and 3.

Koalas

In koalas, the scalenus anterior muscle, which is anterior to the roots of the brachial plexus in humans, was not observed. The superficial part of the scalenus muscle, being posterior to the brachial plexus and arising from the posterior tubercles of the transverse processes of the third and fourth cervical vertebrae, ran down ventral to the cranial digitations of the serratus anterior muscle and was attached to the third

Table 1 Materials

Order	Species	Specimen no.	Sex	Side	Source
Marsupialia	Koala (<i>Phascolarctos cinereus</i>)	No. 1	Female	Both sides	University of Queensland (Australia) (no. Q-UNI1091)
		No. 2	Female	Left side	Australian Museum (Australia) (no. M14074)
Placentalia	Cat (<i>Felis domestica</i>)	No. 32	Male	Right side	Kumamoto University (Japan)
		No. 32	Male	Right side	Kumamoto University (Japan)

Table 2 The attachments and innervations of scalenus muscles

Species	Scalenus			Scalenus longus			
	Origin	Insertion	Insertion	Origin	Insertion	Innervation	
Koala	C2–7 transv. proc.	C3–7 transv. proc.	1st rib	C5–7+? [1d] C5,6+? [1s] C6–8+? [2s]	C3, 4 transv. proc.	C3, 4 transv. proc.	Branches to scalenus
Cat	C1?,2?, 3–7 transv. proc.	C3–7 transv. proc. 1st rib	C6+?	Same as scalenus	3rd+4th, 4th, 8th–10th ribs [32d] 3rd+4th, 5th–8th ribs [35d]	C7, T2, 3 (Rcl) [32d] C7, 8, T2, 3 (Rcl) [35d]	

C: cervical vertebra (Origin and Insertion) or cervical nerve (Innervation), T: thoracic vertebra (Origin and Insertion) or thoracic nerve (Innervation)

The numbers in square brackets are the specimen no.

?, unconfirmed

Table 3 The attachments and innervations of dorsal shoulder girdle muscles

Species	Rhomboides			Levator scapulae			Levator scapulae		
	Origin	Insertion	Innervation	Origin	Insertion	Innervation	Origin	Insertion	Innervation
Koala	Occipital bone Nuchal lig. T1 spin. proc.	Med. border (scapula)	C3,4,5 [1d,s] C4,5 [2s]	C1–7 transv. proc. [1s, 2s] C2–7 transv. proc. [1d]	Sup. angle Med.border (Scapula)	C4, 5 [1d,s] C3, 4, 5 [2s]	1st–7th ribs [1s, 2s] 1st–6th ribs [1d]	Med. border (scapula)	C6,7+T1 (Rcl) [1s] C5,6,7+T1 (Rcl) [1d] C5,6,7,8+T1 (Rcl) [2 s]
Cat	Occipital bone Nuchal lig. C7–T4 spin. proc.	Med. border (scapula)	C4, 5, 6	C3–7 transv. proc.	Sup. angle Med. border (Scapula)	C5 6	1st–9th ribs	Med. border (scapula)	C7 [32d] C7, 8 [35d]

Numbers in square brackets are the specimen no.

(two cases: scl in Fig. 1) or second ribs (one case). In this study, this superficial and long part of the scalenus muscle is defined as the scalenus longus muscle.

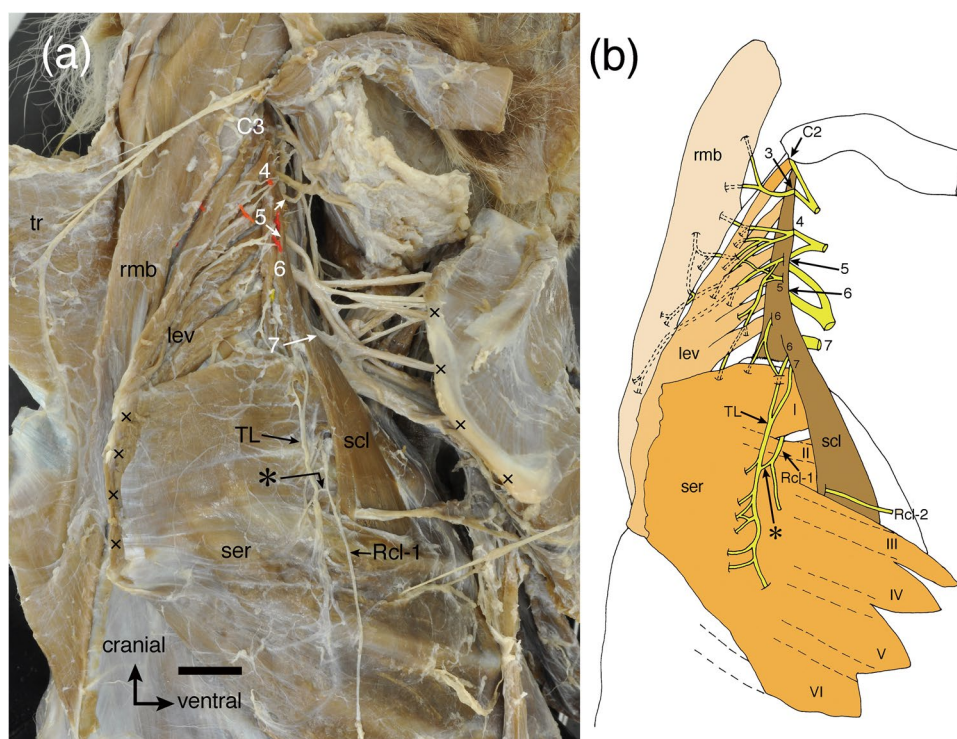
The nerves innervating the dorsal shoulder girdle muscles originated from the dorsal-most layer of each root of the brachial plexus. The nerves to the rhomboides muscles were from C3–5 (two cases, Fig. 1) or from C4, 5 (one case). The branches from C4 and 5 innervated the muscle, forming the common trunk with the branch to the levator scapulae muscle. The levator scapulae muscles were supplied by the branches from C4, 5 (2 cases) or C3–5 (one case). The long thoracic nerve, innervating most of the serratus anterior muscle, branched off from C6, 7 (two cases, Fig. 1) or C5–8 (one case). Each root penetrated independently into the scalenus muscle and joined together on the serratus anterior muscle. Besides the long thoracic nerve, the branch from C5 (two cases, Fig. 1) that innervated the lower bundles of the levator scapulae, or the independent branch from C6 (one case), also supplied the cranial margin of the serratus

anterior muscle. Additionally, in all cases the long thoracic nerve received the branch from the lateral cutaneous nerve of the first intercostal nerve (Rcl-1) on the external surface of the serratus anterior (asterisk in Fig. 1). This Rcl-1 passed through between the first (origin; first rib) and second (origin; second rib) digitations of the serratus anterior to supply the skin. Observed under stereomicroscope, the nerve fibers included in this branch from Rcl-1 were confirmed to supply the lower four (two cases, Fig. 2) or five (one case) digitations of the serratus anterior muscle.

Cats

The levator scapulae and serratus anterior muscles were a continuous muscular sheet, with origins from the cervical vertebrae to the upper ribs. In this study, the upper part that arose from the transverse processes of the cervical vertebrae was identified as the levator scapulae, and the lower part as having its origins from ribs as the serratus

Fig. 1 Photograph (a) and drawing (b) showing the right cervical and upper thoracic trunk muscles and nerves in a koala (no. 1 specimen). Lateral view. **a** Scapula is dissected ventrally to expose the dorsal shoulder girdle and scalenus longus muscles. Asterisk denotes the communication from the lateral cutaneous branch of the first intercostal nerve (*Rcl-1*) to the long thoracic nerve (*TL*). Scale bar: 10 mm. **b** The anterior limb is detached from the trunk with cutting off the brachial plexus. C3–7 ventral rami of the third to seventh cervical nerves, I–VI six muscular digitations of the serratus anterior muscle (*ser*), *lev* levator scapulae muscle, *rmb* rhomboideus muscle, *scl* scalenus longus muscle, *tr* trapezius muscle



anterior. In cats, the scalenus anterior muscle observed in humans was not found. As in koalas, the superficial bundle of the scalenus muscle, defined as the scalenus longus, descended caudally, running superficially to the cranial digitations of the serratus anterior, and split into two (Fig. 3) or three (Figs. 4, 5) bundles. The additional muscular slips (asterisk in Fig. 3) from the scalenus longus muscles were found. However, these slips were separated by the fine tendinous line from the scalenus longus muscle and also received the different nerves from the scalenus longus muscle. Therefore, these muscular slip/slips can be understood as different muscles from the scalenus longus muscles.

Similar to koalas, the nerves innervating the dorsal shoulder girdle muscles were from the dorsal-most layer of each root of the brachial plexus. The nerves to the rhomboideus muscles arose from C4–6 and pierced the levator scapulae muscles in all cases (Fig. 4). The levator scapulae muscles were supplied by the branches from C5 and 6, both of which formed the common trunk with the branches to the rhomboideus muscle. The long thoracic nerve arose from C7 (one case, Fig. 5) or from C7 + 8 (one case, Fig. 3) and pierced the deep part of the scalenus muscle to innervate the serratus anterior from its external surface. The scalenus longus muscles were innervated by the branches from the long thoracic nerve

(double asterisks in Fig. 5) and from Rcl-2 and -3 (single asterisk in Fig. 5).

Origin of the nerve fibers in each spinal root

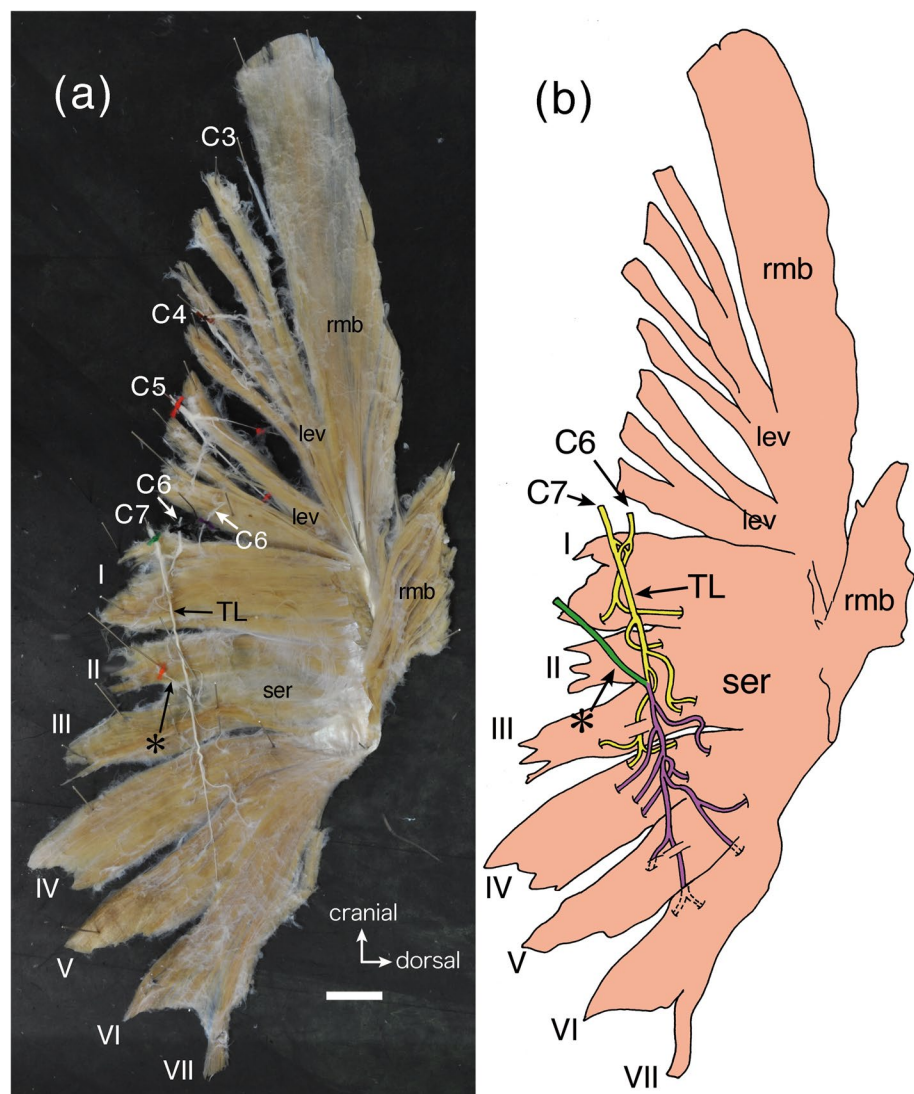
Koalas

The nerve fibers included in the branches to the dorsal shoulder girdle muscles and in the branch to the serratus anterior from Rcl-1 were followed up to each spinal root under the stereomicroscope. In all cases, the nerve to the dorsal shoulder girdle muscles from C5 and 6 (asterisk in Fig. 6) arose from the dorsal-most layer of the ventral ramus near the bifurcation point of the dorsal ramus. Similarly, in the spinal roots of T1 and T2, the nerve fibers to the external intercostal muscle (*Ite-e* in Figs. 7–9) and to the serratus anterior from Rcl-1 (asterisk in Figs. 7, 8) both originated from the dorsal-most layer of the ventral ramus (intercostal nerve) near the bifurcation point of the dorsal ramus.

Cats

In one case, the nerve fibers included in the branches to the dorsal shoulder girdle muscles and the branches to the scalenus longus muscles from Rcl-2, -3 were followed up to each spinal root under the stereomicroscope. The nerves to the rhomboideus muscle from C4, the rhomboideus, and levator

Fig. 2 Photograph (a) and drawing (b) of the left dorsal shoulder girdle muscles and their nerves in a koala (no. 1 specimen). Superficial aspect. Asterisk (green in b) denotes the communicating twig from the lateral cutaneous branch of the first intercostal nerve to the long thoracic nerve (TL, yellow in b). Purple branches in b include both fibers of TL and asterisk. Scale bar: 10 mm. I–VII Digitations of the serratus anterior muscle (*ser*). Other abbreviations are the same as in Fig. 1



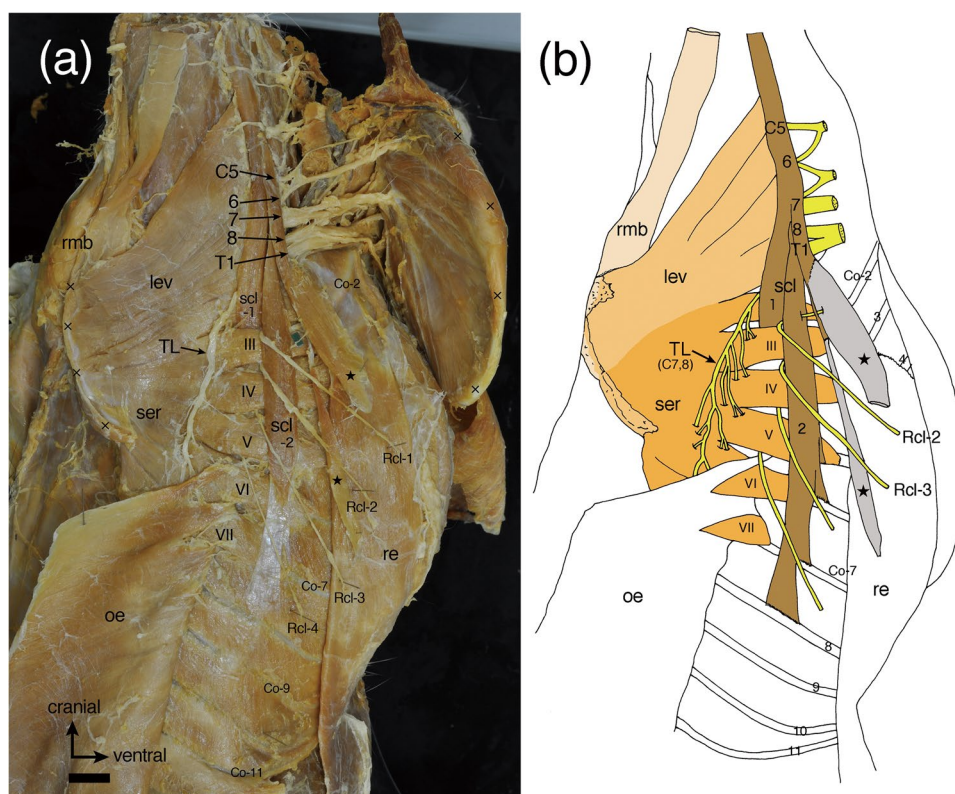
scapulae muscles from C5 and C6, and the serratus anterior muscle (long thoracic nerve) from C7 had their origins in the dorsal-most layer of the ventral ramus near the bifurcation point of the dorsal ramus (Fig. 10). The nerves to the scalenus longus muscles arising from Rcl-2,3 (*scl* in Fig. 11) arose from the dorsal-most layer of the ventral ramus (intercostal nerve) near the bifurcation point of the dorsal ramus with forming of the common trunk with the branches to the external intercostal and supracostal muscles.

Discussion

The levator scapulae, rhomboideus, and serratus anterior muscles are all innervated by the branches arising from the dorsal-most layer of the ventral rami of the cervical nerves and are understood to belong to the same group as the dorsal shoulder girdle muscles (Bolk 1902; Eisler 1912; Howell

1936; Nishi 1938; Braus and Elze 1954; Romer and Parsons 1977; Kato 1989). The embryological study by Lewis (1902) showed that the levator scapulae and serratus anterior muscles are differentiated from the common muscular mass and that the rhomboideus muscle developed later from this common mass. The morphological significance of these dorsal shoulder girdle muscles among the somite-derived muscles innervated by the spinal nerves has also been discussed. Howell (1936) classified the trunk muscles into dorsal and lateroventral divisions, with the former division innervated by the dorsal ramus of the spinal nerve and the latter innervated by the ventral ramus. In addition, he considered that the dorsal shoulder girdle muscles belonged to the dorsal scapular group of the appendicular system in the lateroventral division and distinguished these muscles from the scalenus and intercostalis muscles that belonged to the axial system. Braus and Elze (1954) grouped the dorsal shoulder girdle muscles into the “Dorsale Gruppe der

Fig. 3 Photograph (a) and drawing (b) showing the right cervical and upper thoracic trunk muscles and nerves in a cat (no. 35 specimen). Lateral view. **a** The muscular attachment of the medial border of the scapula (times) is cut off and the scapula is dissected down ventrally. The obliquus externus abdominis muscle (*oe*) is reflected dorsally to show the insertion of the scalenus longus-2 muscle (*scl-2*). The additional muscles indicated by a *star* are mentioned in the text. Scale bar: 10 mm. **b** The anterior limb is detached from the trunk with cutting off of the brachial plexus. *III–VII* Digitations of the serratus anterior muscle (*ser*), *Co* costa, *oe* obliquus externus abdominis, *re* rectus abdominis muscle, *TL* ventral ramus of the first thoracic nerve. Other abbreviations are the same as in Fig. 1



eingewanderten Rumpfmuskulatur (dorsal group of the migrated trunk muscles),” while they believed that the scalenus and intercostal muscles were grouped into a different group, the “ventrolateral Rumpfmuskulatur (ventrolateral trunk muscles).” To the contrary, Romer and Parsons (1977) considered the dorsal shoulder girdle muscles as “trunk muscles of the shoulder region” and Stark (1982) considered them to be “die axialen Muskeln zwischen Rumpf Schädel and Schultergürtel (axial muscle between thorax and shoulder girdle).” Both sets of authors thought that the dorsal shoulder girdle muscles belonged to the axial muscles, not to the limb muscles. This notion was confirmed by embryological studies that indicated that the dorsal shoulder girdle muscles expressed the same developmental pattern as the axial muscles, such as the intercostal muscles, and not as the limb muscles (Prunotto et al. 2004; Valasek et al. 2010). The morphological relationship between the dorsal shoulder girdle muscles and other axial muscles in the cervico-thoracic regions has also been discussed by some authors. Nishi (1938), in his study on the homology among trunk muscles in the cervico-thoracic regions, described the dorsal shoulder girdle muscles as belonging to the “Obliquus externus group” of the “Ventrale Rumpfmuskulatur (ventral trunk muscle),” such as the external intercostal muscle, and the scalenus muscles as belonging to both the “obliquus externus group” and “obliquus internus group.”

When discussing the homology of muscles, it is important to determine just what criteria are used. Romer and Parsons (1977), in their textbook of comparative anatomy, discuss the homology of muscles based mainly on the positional relationships and functions of muscles. On the other hand, Nishi (1961) described that the innervation is the most reliable criterion on which to base a discussion on the homology of muscles. Although Diogo et al. (2009) mentioned that there were cases in which the same muscle had different innervations in different taxa, there have in fact been many excellent studies that have clarified the morphological significance and phylogenetic homology of muscles based on innervations (Kato and Sato 1984; Yamada 1986; Kodama 1986; Murakami 1988; Koizumi and Sakai 1995; Sakamoto et al. 1996; Honma et al. 1998; Koizumi et al. 2002; Kawashima et al. 2003; Arakawa et al. 2006). Kodama (1986) and Sakamoto et al. (1996) advanced these previous studies and clarified the morphological significance of the thoracic and abdominal trunk muscles on the basis of the topographical relationship between the muscles and the intercostal nerves, and of the branching patterns of each muscular branches. Tokiyoshi et al. (2004) observed the ramifications of each muscular branch of the intercostal nerve in the spinal roots and confirmed that the nerve fibers to the external intercostal muscle occupied the dorsal-most layer of the motor component of the intercostal nerve, a

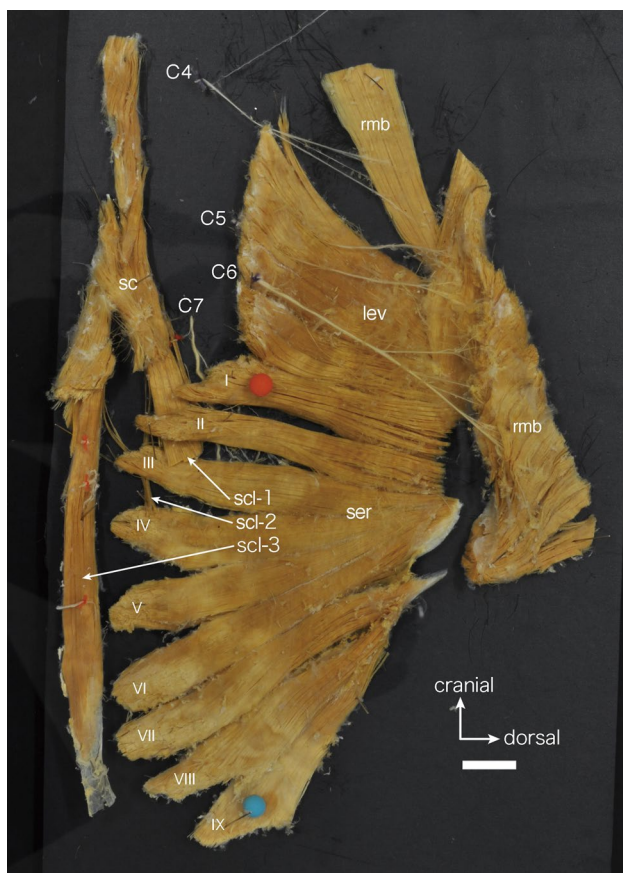


Fig. 4 Photograph of the right dorsal shoulder girdle and scalenus muscles with their nerve supply in the other cat (no. 32 specimen). Superficial aspect. *scl-1*, -2, -3 Three muscular bundles of the scalenus longus muscle. *I-IX* Nine muscular digitations of the serratus anterior (*ser*). Scale bar: 10 mm. *C4-7* ventral rami of the fourth to seventh cervical nerves, *sc* scalenus muscle. Other abbreviations are the same as in Fig. 1

finding which agrees with the results of the present study. Kodama (1986) and Tokiyoshi et al. (2004) discussed the morphological relationship between the cervical and thoracic trunk muscles. However, they did not refer to the dorsal shoulder girdle muscles because they thought that the dorsal shoulder girdle muscles belonged to the limb muscles, not to the axial trunk muscles.

The cervical trunk muscles and intercostal muscles are usually innervated by the segmentally different nerves, namely, the cervical and thoracic nerves, respectively; therefore, the homology of both muscles can not be discussed directly by their innervations. However, in the present study, the findings that the dorsal shoulder girdle and scalenus muscles in koalas and cats, innervated usually by the cervical nerves, additionally received the intercostal nerves clearly shows the morphological relationship between the cervical axial and the intercostal muscles. Figure 12 is the schematic diagram showing

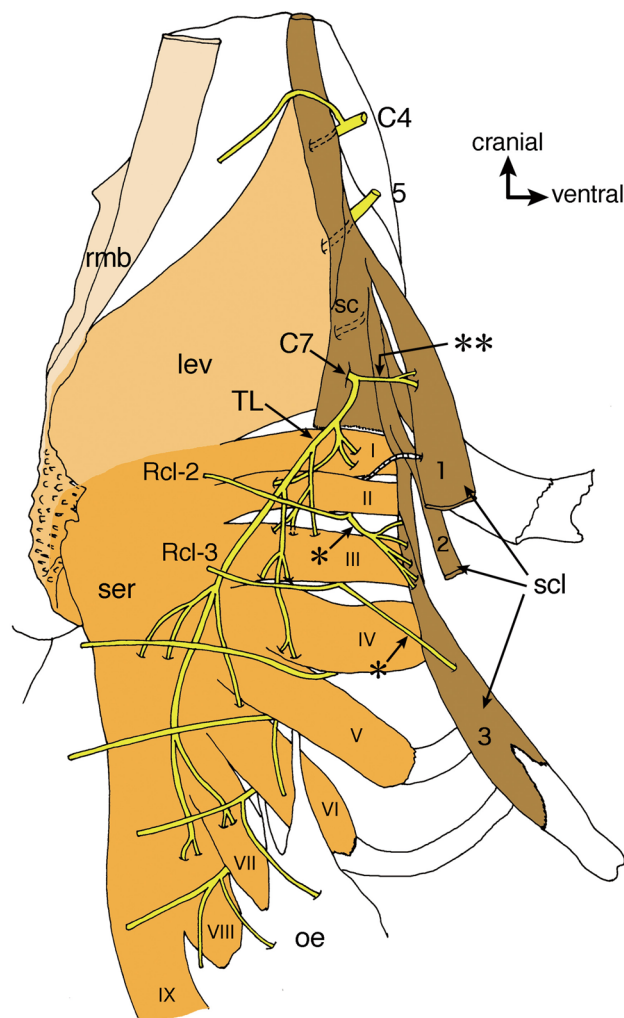


Fig. 5 Diagram of the right dorsal shoulder girdle and scalenus longus muscles with their innervation in the same specimen as shown in Fig. 4. Lateral view. The insertions of the three bundles of the scalenus longus (*scl-1*, -2, -3) are cut off and reflected ventrally to show the nerve supplies (asterisk and double asterisk). *I-IX* Muscular digitations of the serratus anterior muscle. Other abbreviations are the same as in Fig. 1

the spinal root origins of the nerve fibers innervating the dorsal shoulder girdle and scalenus muscles. In both the cervical and thoracic nerves, all of the nerve fibers to the levator scapulae, rhomboideus, serratus anterior, and scalenus longus muscles arise from the dorsal-most layer of the ventral rami, just like the branches to the external intercostal muscles. According to neurological studies that have clarified the topographic organization in the spinal cord of the motoneurons supplying the shoulder and trunk muscles in rats, cats, or chicken (Smith and Hollyday 1983; Hörner and Kümmel 1993; Gutman et al. 1993; Tani et al. 1994; Izumi and Kida 1998), the relative ventral to dorsal position of muscles is reflected in the relative medial to lateral position of motoneurons

Fig. 6 Photograph (a) and diagram (b) of the left fifth (C5) and sixth (C6) cervical nerve roots in a koala (no. 2 specimen). Dorsal view. Asterisk denotes the branch innervating the dorsal shoulder girdle muscles. Scale bar: 5 mm. *D* Dorsal root, *dors* dorsal ramus, *V* ventral root, *vent* ventral ramus

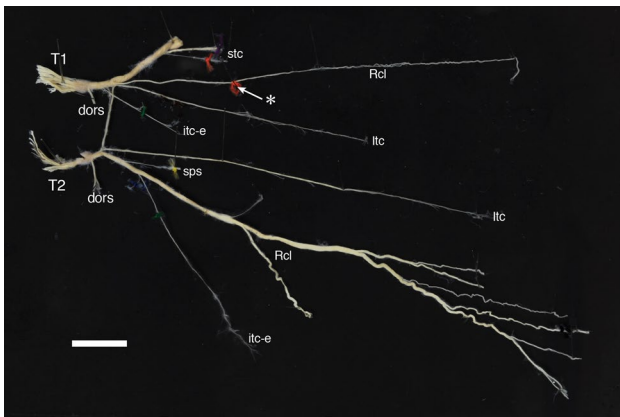
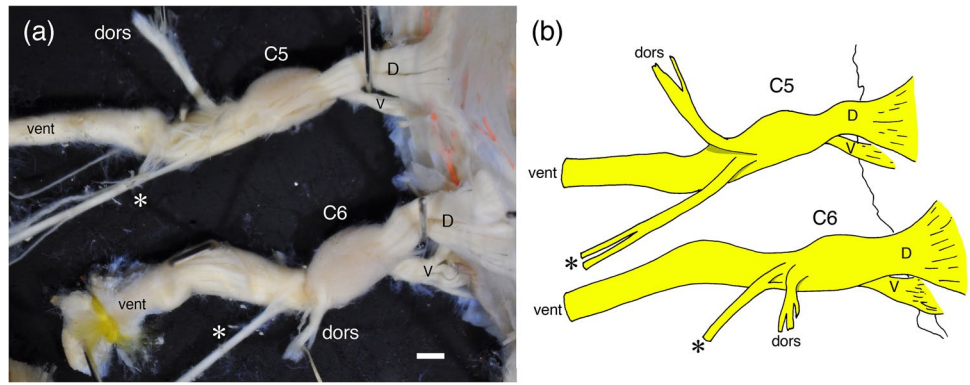


Fig. 7 Photograph of the branching pattern of the right first (T1) and second (T2) thoracic nerves in a koala (no. 1 specimen). Dorsal view. The muscles supplied by T1 and T2 are all removed. Asterisk denotes the branch that innervates the serratus anterior muscle together with the thoracic nerve. Scale bar: 10 mm. *D* Dorsal root, *dors* dorsal ramus, *Itc* intercostal nerve, *itc-e* external intercostal muscle, *Rcl* lateral cutaneous branch, *sps* serratus posterior superior muscle, *stc* sternocostalis muscle, *V* ventral root

innervating them in the ventral horn of the spinal cord. Hörner and Kümmel (1993) mentioned that motor cell clusters appear to be arranged very similarly in different vertebrates, leading these authors to suggest that the topography of spinal motor nuclei is independent of both the position and the functions of the target muscles, but dependent on their phylogenetic origin. In cats, the spatial orientation of the motoneuron pools supplying the thoracic trunk muscles was thought to be clearly reflected by the ramification pattern of the spinal nerves of the intercostal nerves (Tani et al. 1994). In fact, the motoneurons innervating the external intercostal muscle occupied the center of the ventral horn contiguous to the motoneuron clusters supplying the epaxial muscles (Smith and Hollyday 1983), and the nerve to the external intercostal muscle branches off from the dorsal-most layer of the intercostal nerve just ventral to the dorsal ramus supplying the epaxial muscles, as shown in this study. Therefore, the branching pattern of the spinal nerves at the spinal roots can be thought to be an important criterion for discussing the homology of trunk muscles.

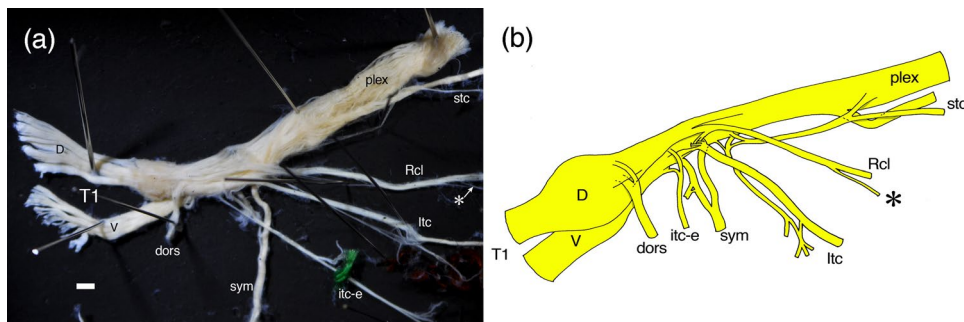


Fig. 8 Enlarged photograph (a) and diagram (b) of the first thoracic nerve (T1) root in the same specimen as shown in Fig. 7. Dorsal view. Asterisk denotes the branch that innervates the serratus anterior mus-

cle together with the thoracic nerve. Scale bar: 1 mm. *plex* Branch contributing to the brachial plexus, *sym* communicating branch with the sympathetic trunk. Other abbreviations are the same as in Fig. 7

Fig. 9 Enlarged photograph (a) and diagram (b) of the second thoracic nerve (T2) root in the same specimen as shown in Fig. 7. Dorsal view. Scale bar: 1 mm. *sps* Serratus posterior superior muscle. Other abbreviations are the same as in Fig. 10

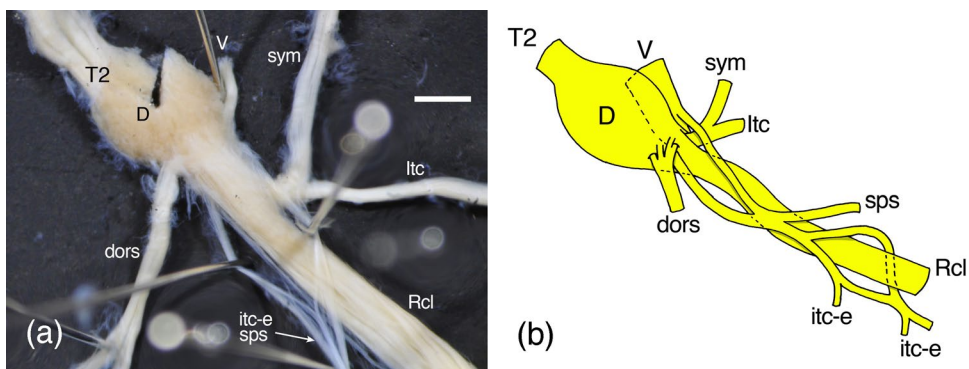
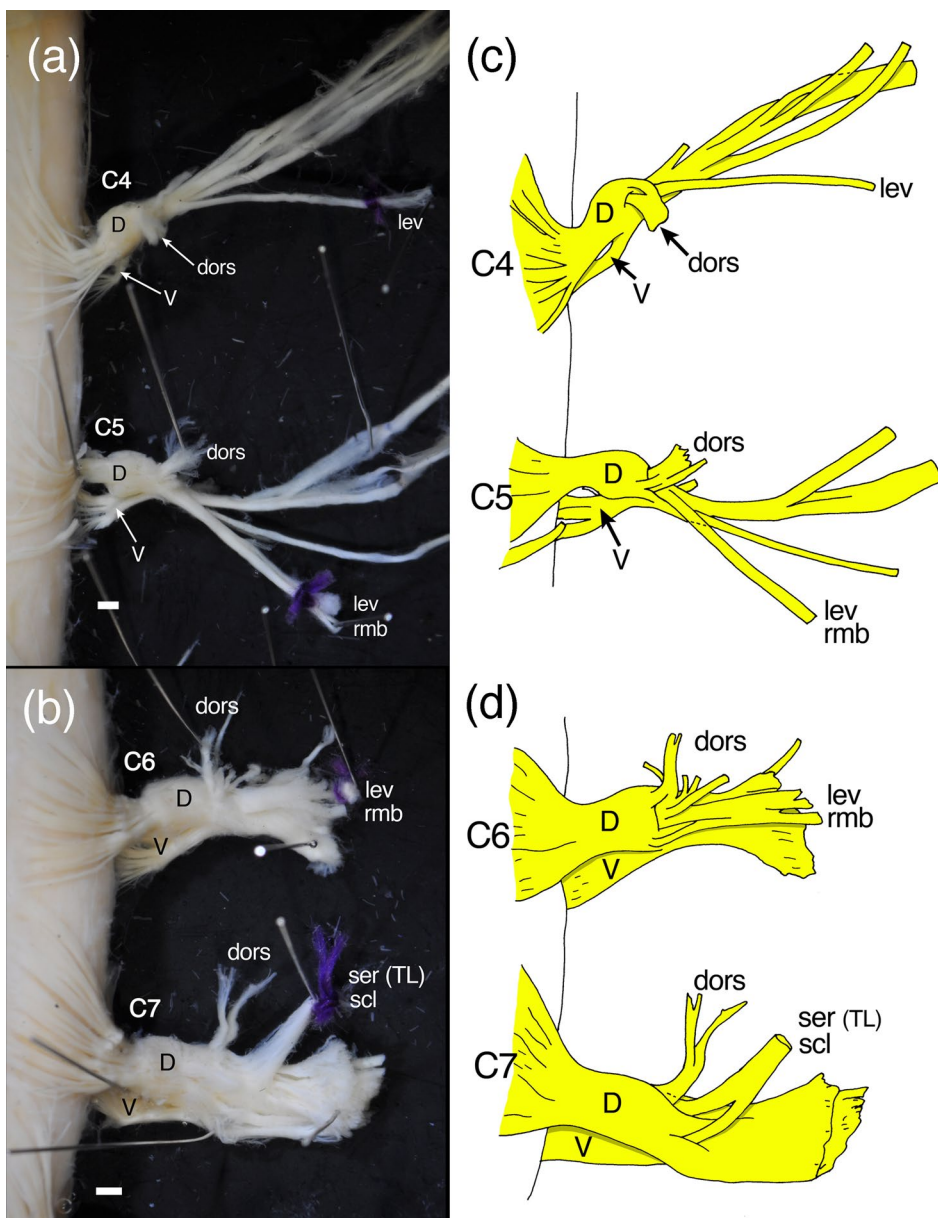


Fig. 10 Photographs (a, b) and diagrams (c, d) of the lower four cervical nerve roots (C4–7) in the same cat as shown in Fig. 5. Dorsal aspect. Scale bars: 1 mm. *D* Dorsal root, *dors* dorsal ramus, *lev* levator scapulae muscle, *rmb* rhomboid muscle, *ser (TL)* serratus anterior muscle (long thoracic nerve), *scl* scalenus longus muscle, *V* ventral root



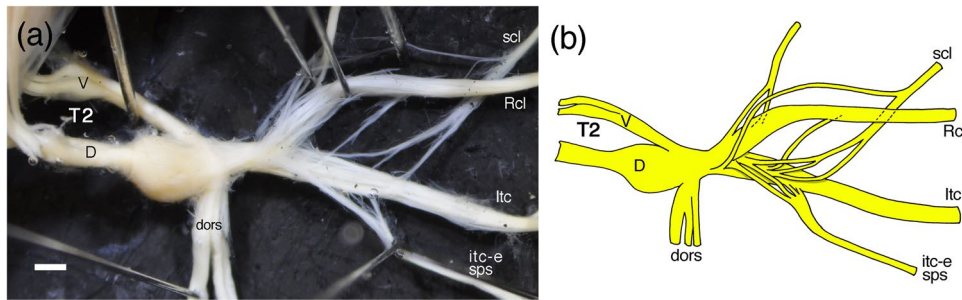


Fig. 11 Enlarged photograph (a) and diagram (b) of the second thoracic nerve root (*T2*) in the same specimen as shown in Fig. 5. Dorsal view. *scl* Branch that innervates the scalenus longus muscle. Scale

bar: 1 mm. *Itc* intercostal nerve, *itc-e* external intercostal muscle, *Rcl* lateral cutaneous branch, *sps* serratus posterior superior muscle. Other abbreviations are the same as in Fig. 10

Based on these observations, schematic diagrams showing the cross-sectional arrangement of the trunk wall muscles in the cervical and thoracic regions have been drawn up (Fig. 13). In the thoracic region (Fig. 13a), the intercostal nerve (yellow), which is the ventral ramus of the thoracic nerve, runs between the internal and innermost intercostal muscles, supplying both muscles and innervating the rectus abdominis muscle to end as the anterior cutaneous nerve. The nerve fibers included in the lateral cutaneous branch (orange) could be separated from the intercostal nerve fibers up to the spinal root. The fact that the nerve fibers to the serratus anterior (in koalas) and scalenus longus (in cats) muscles that are included in the lateral cutaneous branch have the same origin as the branch to the external intercostal muscle (red) indicates that the serratus anterior and scalenus longus muscles can be considered to belong to the same group as the external intercostal muscle. The reason why these nerve fibers take the course in the lateral cutaneous branch, and not in the branch to the external intercostal muscle, is not yet definite, but two possibilities have been suggested (Murakami 1988;

Sakamoto et al. 1996). According to Murakami (1988), in crocodiles, the trunk muscle that might be considered to be homologous with the external intercostal muscle in mammals is separated into dorsal and ventral parts. The dorsal part is innervated by the branch that is homologous to the nerve supplying the mammalian external intercostal muscle and the ventral part is innervated by the nerve from the lateral cutaneous branch. Sakamoto et al. (1996) reported their observation of a twig that had branched off from the lateral cutaneous branch to supply the ventral portion of the external intercostal muscle in humans. They suggested that the dorsal and ventral parts in crocodiles were completely fused in mammals to form the single external intercostal muscle. The results of these comparative anatomical studies suggest that a part of the serratus anterior muscle in koalas and a part of the scalenus longus muscle in cats, both of which are innervated by the lateral cutaneous branch, are homologous to the ventral part of the external intercostal muscle in crocodiles. Furthermore, judging from the origins of each branch in the spinal roots, the nerves to the dorsal shoulder girdle and scalenus muscles (Fig. 13b; red) can be considered to be homologous with the branch to the external intercostal muscle (Fig. 13a; red).

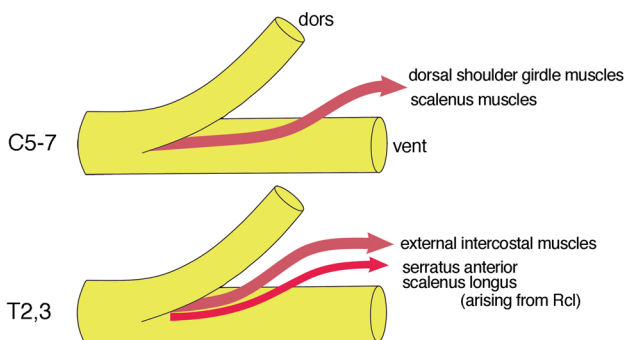


Fig. 12 Schematic diagrams showing the origins of the branches to the external intercostal, scalenus, and dorsal shoulder girdle muscles in koalas and cats. Dorsal aspect. *dors* Dorsal ramus, *T1, 2* first and second thoracic nerves, *vent* ventral ramus

In conclusion, the thoracic wall muscles can be classified into the medial group (Fig. 13; green) that is innervated by the branches from the intercostal nerve trunk and the lateral group (Fig. 13; blue) innervated by the branch arising from the dorsal-most layer of the root of the intercostal nerve. The internal/innermost intercostal and rectus abdominis muscles belong to the medial group. The external intercostal muscle in the thoracic region and the dorsal shoulder girdle (including the serratus anterior in koalas) and scalenus muscles

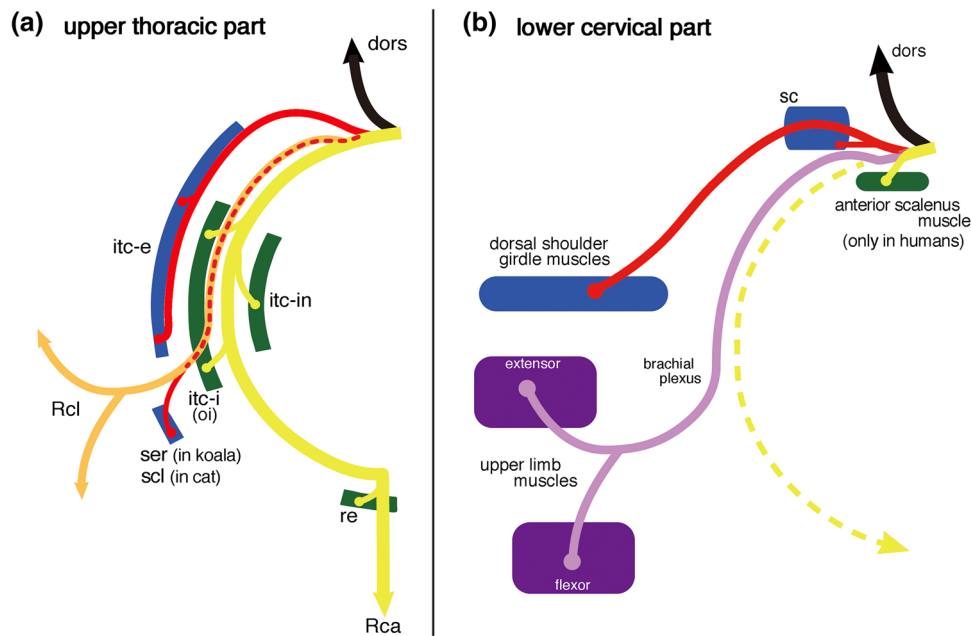


Fig. 13 Schematic diagrams of the upper thoracic (a) and lower cervical (b) nerves and muscles in cross-section. Blue bars represent the lateral trunk muscle group; green lines represent the medial muscle group; purple lines represent the limb muscle group. In the lower cervical part, the yellow-dotted line indicates the disappeared part corresponding to the distal part of the intercostal nerve in the thoracic

region. Details are provided in the text. *dors* Dorsal ramus, *itc-e* external intercostal muscle, *itc-in* innermost intercostal muscle, *itc-i* internal intercostal muscle, *Rca* anterior cutaneous branch, *Rcl* lateral cutaneous branch, *re* rectus abdominis muscle, *sc* scalenus muscle, *scl* scalenus longus muscle, *ser* serratus anterior muscle

(including the scalenus longus in cats) in the cervico-thoracic region all belong to the lateral group.

Acknowledgements The author specially thanks Dr. M. Yamasaki, formerly of the Department of Anatomy, Akita University, for providing a koala specimen, which was originally from Australian Museum, Sydney, NSW, Australia.

Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

References

- Arakawa T, Sekiya S, Kumaki K, Terashima T (2006) Intramuscular nerve distribution pattern of the oblique and transverse heads of the adductor hallucis muscles in the human foot. *Anat Sci Int* 81:187–196
- Bolk L (1902) Die Beiträge zur Affenanatomie III. Der Plexus Cervico-brachialis der Primaten. *Petrus Camper* 1:371–567
- Braus H, Elze C (1954) *Anatomie des Menschen*. Auflage 3, vol 1. Springer, Berlin
- Buckingham M, Bajard L, Chang T et al (2003) The formation of skeletal muscle: from somite to limb. *J Anat* 202:59–68
- Crouch JE (1969) *Text-atlas of cat anatomy*. Lea & Febiger, Philadelphia

- Diogo R, Abdala V, Aziz A, Lonergan N, Wood A (2009) From fish to modern humans—comparative anatomy, homologies and evolution of the pectoral and forelimb musculature. *J Anat* 214:694–716
- Eisler P (1912) Die Muskeln des Stammes. In: von Bardeleben K (ed) *Handbuch der Anatomie des Menschen*. Band 2. Gustav Fischer, Jena, pp 368–383 (496–504)
- Francis-West PH, Antoni L, Anakwe K (2003) Regulation of myogenic differentiation in the developing limb bud. *J Anat* 202:69–81
- Gutman CR, Ajmera MK, Hollyday M (1993) Organization of motor pools supplying axial muscles in the chicken. *Brain Res* 609:129–136
- Honma S, Jun Y, Horiguchi M (1998) The human gemelli muscles and their nerve supplies. *Acta Anat Nippon* 73:329–335
- Hörner M, Kümmel H (1993) Topographical representation of shoulder motor nuclei in the cat spinal cord as revealed by retrograde fluorochrome tracers. *J Comp Neurol* 335:309–319
- Howell AB (1936) The phylogenetic arrangement of the muscular system. *Anat Rec* 66:293–316
- Izumi A, Kida MY (1998) Segmental distribution of the motoneurons innervating trunk muscles in the spinal cord of the cat and rat. *Neurosci Res* 30(3):247–55
- Kato K (1989) Innervation of the scapular muscles and its morphological significance in man. *Anat Anz* 168:155–168
- Kato K, Sato T (1984) Innervation of the levator scapulae, the serratus anterior, and the rhomboideus in crab-eating macaques and its morphological significance. *Anat Anz* 157:43–55
- Kawashima T, Yoshitomi S, Ito M et al (2003) Bilateral aberrant biceps brachii muscles with special reference to their common nerve trunks. *Okajimas Folia Anat Jpn* 80:77–84
- Kodama K (1986) Morphological significance of the supracostal muscles, and the superficial intercostal nerve—a new definition. *Acta Anat Nippon* 61:107–129 (in Japanese with English abstract)

- Koizumi M, Sakai T (1995) The nerve supply to coracobrachialis in apes. *J Anat* 186:395–403
- Koizumi M, Kawai K, Honma S, Kodama K (2002) Anomalous lumbrical muscles arising from the deep surface of flexor digitorum superficialis muscles in man. *Ann Anat* 184:387–392
- Lewis WH (1902) The development of the arm in man. *Am J Anat* 1:145–184
- Murakami G (1988) Nerve supply of the ventral trunk musculature of the brown caiman (*Caiman crocodilus fuscus*: Alligatoridae, Crocodylia), and its morphological consideration. *Acta Anat Nippon* 63:20–52 (in Japanese with English abstract)
- Nishi S (1938) Muskeln des Rumpfes. In: Bolk L, Göppert E, Kallius E, Lubosch W (eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, vol 5. Urban & Schwarzenberg, Berlin, pp 351–446
- Nishi S (1961) Typologische Anatomie des Muskelsystem. *Acta Anat Nippon* 48:137–145 (in Japanese)
- Prunotto C, Crepaldi T, Forni PE et al (2004) Analysis of *Mlc-lacZ* Met mutants highlights the essential function of Met for migratory precursors of hypaxial muscles and reveals a role for Met in the development of hyoid arch-derived facial muscles. *Dev Dyn* 231:582–591
- Romer AS, Parsons TS (1977) *The vertebrate body*, 5th edn. WB Saunders, Philadelphia
- Sakamoto H, Akita K, Sato T (1996) An anatomical analysis of the relationships between the intercostal nerves and the thoracic and abdominal muscles in man. I. Ramification of the intercostal nerves. *Acta Anat* 156:132–142
- Smith CL, Hollyday M (1983) The development and postnatal organization of motor nuclei in the rat thoracic spinal cord. *J Comp Neurol* 220:16–28
- Stark D (1982) *Vergleichende Anatomie der Wirbeltiere auf evolutionsbiologischer Grundlage*, vol 3. Springer, Berlin
- Tani M, Kida MY, Akita K (1994) Relationship between the arrangement of motoneuron pools in the ventral horn and ramification pattern of the spinal nerve innervating trunk muscles in the cat (*Felis domestica*). *Exp Neurol* 128:290–300
- Tokiyoshi A, Koizumi M, Kawai K, Honma S, Takagi K, Kodama K (2004) Scalenus muscles in macaque monkeys. *Anat Sci Int* 79:32–42
- Valasek P, Theis S, Krejci E et al (2010) Somitic origin of the medial border of the mammalian scapula and its homology to the avian scapula blade. *J Anat* 216:482–488
- Yamada TK (1986) Re-evaluation of the flexor digitorum superficialis. *Acta Anat Nippon* 61:283–298 (in Japanese with English abstract)

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.