Functional morphology of the forelimb muscles in an aardvark

Hideki Endo^{1,*}, Takeo Sakai², Takuya Itou², Hiroshi Koie³, Junpei Kimura⁴, Motoki Sasaki⁵, Brian J. Stafford⁶, Masako Yamamoto⁷ and Kazuyoshi Arishima⁷

¹ Department of Zoology, National Science Museum, Tokyo, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan

² Department of Preventive Veterinary Medicine and Animal Health, ³ Laboratory of Comprehensive Veterinary Clinical Studies and ⁴ Department of Veterinary Anatomy, College of Bioresource Sciences, Nihon University, Fujisawa, Kanagawa, Japan

⁵ Department of Veterinary Anatomy, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Hokkaido, Japan

⁶ Mammal Division, National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.

⁶ Department of Anatomy, Howard University College of Medicine, Washington DC, U.S.A.

⁷ Department of Veterinary Anatomy II, Azabu University School of Veterinary Medicine, Sagamihara, Kanagawa, Japan

Abstract. The muscles of the forelimb were functional-morphologically examined in a carcass of the aardvark (*Orycteropus afer*) that is highly adapted to the fossorial life and the digging behavior. The *M. pronator quadratus*, the *M. abductor digiti I longus*, the *M. brachioradialis*, the *M. pronator teres* and the *M. supinator* are well-developed. We suggest that the supinator-pronator movement by these muscles enables the aardvark to dig, crush and sweep the soils in its fossorial behavior. In addition, the *M. extensor digiti II* runs obliquely to rotate the forearm around the ulna shaft. We think that this muscle may not only function as an extensor of the digits II and III, but also as a supinator of the forearm. Many extensor muscles can be separated into two groups on the basis of their insertion. The *M. extensor digiti II* and the *M. extensor carpi radialis* insert to the digits-metacarpals II–III, whereas the *M. extensor digitorum lateralis* and *M. extensor carpi ulnaris* reach the digits-metacarpals IV–V. We suggest that the crushing of the soil is accomplished by the two medial digits and that the lateral two digits mainly act as a remover or a sweeper of the crushed soil.

Key words: aardvark, digging action, forearm, *Orycteropus afer*, skeletal muscle.

The aardvark is a highly adapted species of mammals to fossorial life and digging action. The structure of the limbs has attracted many anatomists and has been described in some studies (Galton 1868; Sonntag 1925; Shrivastava 1962; Jouffroy 1971; Thewissen and Badoux 1986). However the functional advantage of the forearms as digging apparatus has remained unclear in this species. Therefore, in this study, we detailed the forearm muscles that contribute to the digging action and fossorial behavior, using a rare carcass donated from a zoo.

Material and methods

We used a carcass of one aardvark (*Orycteropus afer*) that had been donated to the National Science Museum,

Tokyo, by Ueno Zoological Gardens (Tokyo, Japan). It was about 3 years old female and 950 cm in head and body length. Fixation was avoided so that the skeletal specimen could be well prepared after the examination. The muscles in the forearm were dissected and observed by naked eyes. The functional significance of the forearm muscles was discussed. The specimen number of the individual is NSMT-M31995.

Results

Extensor group

In the superficial layer, the *M. brachioradialis* were enlarged in the anterior area of the forearm (Fig. 1). The belly from the postero-proximal and latero-proximal sur-

* To whom correspondence should be addressed. E-mail: endo@kahaku.go.jp

Fig. 1. Antero-lateral aspect of left forearm. The *M. brachioradialis* (B) is enlarged in the anterior-medial position. The *M. extensor digitorum communis* (C) and the *M. extensor carpi ulnaris* (U) can be seen. The *M. extensor digitorum lateralis* possesses the medial (1) and the lateral (2) heads.

Fig. 2. Anterior aspect of left carpal and metacarpal regions. The *M. extensor digitorum communis* (C) send the tendons to each proximal phalanx. The medial (1) and lateral (2) heads of the *M. extensor digitorum lateralis* can be observed. The *M. brachioradialis* (B) inserts medially to the radius (arrow) and laterally to the *Extensor retinaculum* (arrowhead). S, the second metacarpal. F, the fifth metacarpal.

Fig. 3. Anterior aspect of left forearm and palm regions. The *M. extensor digitorum communis* (C) send the tendons to each proximal phalanx. In the deeper layer, *M. extensor carpi radialis* (R) and *M. supinator* (S) can be seen. The enlarged *M. abductor digiti I longus* (asterisk) medially runs to the first carpal bone. The thin distal part of the *M. abductor digiti I longus* (arrow) passes the space beneath the *M. brachioradialis* (B). 2, the lateral head of the *M. extensor digitorum lateralis*.

Fig. 4. Lateral aspect of left forearm and palm regions. Beneath the medial (1) and lateral (2) heads of the *M. extensor digitorum lateralis* and the *M. extensor carpi ulnaris* (U), the thin *M. extensor digiti II* (arrows) runs medially. The flat bundle of the *M. abductor digiti I longus* (asterisk) can be seen. C, the *M. extensor digitorum communis*.

faces of the humerus was flat and large, became tendinous and possessed the insertion on the medial surface of the radius and in the proximal side of the *Extensor retinaculum* (Fig. 2). The *M. extensor digitorum communis* originated from the lateral epicondyle of the humerus, ran in dorsal area of the forearm, and sent the tendons to the proximal phalanges II, III, IV and V (Figs. 1 and 2). This muscle represented the thickest belly in extensor group. In the lateral side, the *M. extensor digitorum lateralis* and the *M. extensor carpi ulnaris* were observed (Fig. 1). The *M. extensor digitorum lateralis* arose from the lateral epicondyle and was separated into two heads in its entire region. The medial head was attached to the *M. extensor digitorum communis* in its proximal part, and reached the lateral side of the proximal phalanx IV

(Fig. 2). The lateral head from the lateral epicondyle was positioned closely to the *M. extensor carpi ulnaris* in its proximal area (Fig. 1). This head inserted to the lateral side of the proximal phalanx V as a strong tendon. The most lateral extensor was the *M. extensor carpi ulnaris*. This muscle arose from the dorso-proximal surface of the ulna and the lateral epicondyle of the humerus, accompanied the lateral head of the *M. extensor digitorum lateralis* and sent each tendon to the dorso-proximal surface of the fourth and fifth metacarpals.

After removing the *M. brachioradialis*, we confirmed *M. abductor digiti I longus*, *M. extensor carpi radialis* and *M. supinator* (Fig. 3). The well-developed *M. abductor digiti I longus* arose from the anterior surface of the ulna and the antero-proximal surface of the radius,

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Fig. 5. Posterior aspect of left forearm. The *M. flexor digitorum superficialis* (S) occupies the superficial space in this aspect. The thin *Caput humerale* (H) and enlarged *Caput ulnare* (U) of the *M. flexor carpi ulnaris* are discerned.

Fig. 6. Posterior aspect of left forearm. After turning out the *M. flexor digitorum superficialis* (S), the *Flexor retinaculum* (arrowhead) is encountered. The *M. flexor carpi radialis* (R) and *M. pronator teres* (arrow) can be observed in medial area. P, the *M. flexor digitorum profundus*.

Fig. 7. Posterior aspect of left forearm. The *M. flexor digitorum profundus* (P) is well-developed in deeper region beneath the *M. flexor carpi radialis* (R). Arrow, the *M. pronator teres*.

Fig. 8. Posterior aspect of the deepest area of the left forearm. Distal direction at the left. The *M. pronator quadratus* (arrows) runs transversally between the radius and the ulna. R indicates the position of the shaft of the radius. P, the *M. flexor digitorum profundus*.

and occupied the space beneath the *M. brachioradialis*, *M. extensor digitorum communis* and *M. extensor digiti II*. The enlarged bundle overlay the *M. extensor carpi radialis* in the distal area, and sent the tendon to the dorso-lateral side of the first carpal bone (*Os trapezium*). The *M. extensor carpi radialis* sprang from the lateral epicondyle of the humerus (Fig. 3). The muscle consisted of a single thin belly and became thick in the distal area, and sent the two separated tendons to the medio-proximal surface of the second metacarpal and third metacarpal, respectively. The *M. supinator* was long-triangular in anterior aspect, ran from the latero-distal area of the humerus to the proximo-anterior surface of the radius (Fig. 3). The insertion area of the *M. supinator* was close to a part of the origin of the *M. abductor digiti I longus* in the anterior surface of the radius.

After turning out the lateral head of the *M. extensor digitorum lateralis* and the *M. extensor carpi ulnaris*, we discerned the thin *M. extensor digiti II* (Fig. 4). This thin

bundle arose from the lateral surface of the ulna and inserted to the dorso-proximal surface of the second and third metacarpals beneath the tendons of the *M. extensor digitorum communis*. The muscle became completely tendinous in the distal portion.

Flexor group

The *M. flexor digitorum superficialis* represented only one superficial muscle in the posterior side (Fig. 5). The belly ran from the medial epicondyle of the humerus to the palmar surface of the medial phalanges II, III, IV and V. The belly could not be separated into any head and was enlarged in the posterior area of the forearm. The *M. flexor carpi ulnaris* consisted of the two fused heads, the strongest bellies among the flexor group (Fig. 5). The muscle was obviously separated into *Caput humerale* and *Caput ulnare* (Fig. 5). The *Caput ulnare* arose from the medio-proximal surface of the ulna, while the *Caput humerale* originated from the medial epicondyle. The

Caput ulnare was thick and covered by the strong white fasciae in the superficial aspect. The *Caput humerale*, however, was thin and attached to the *M. flexor digitorum superficialis* near its origin. Both heads were fused in the distal area, and inserted to the accessory carpal bone.

After turning out the *M. flexor digitorum superficialis*, the strong *Flexor retinaculum* was encountered (Fig. 6). In the medial area *M. flexor carpi radialis* and *M. pronator teres* could be observed. The *M. flexor carpi radialis* sprang from the medial epicondyle and ran into the palmer surface of the second metacarpals (Fig. 6). The muscle appeared tendinous and was fleshy only in a proximal third of its total length. The *M. pronator teres* arose from the medial epicondyle of the humerus and largely inserted to the medial surface of the radius (Fig. 6). The muscle was thick and occupied the space between *M. flexor carpi radialis* and *M. brachioradialis*. The *M. flexor digitorum profundus* was also seen in this aspect (Fig. 6).

After removing the *Caput humerale* of the *M. flexor carpi ulnaris*, and turning out the *M. flexor carpi radialis*, the entire region of the *M. flexor digitorum profundus* could be seen (Fig. 7). The muscle consisted of the some partially-separated heads. The bellies sprang from the radius, humerus and ulna, and were completely fused in the distal area. Its tendons reached the medio-proximal area of both distal and medial phalanges II, III, IV and V.

Beneath the *M. flexor digitorum profundus* and *M. pronator teres* in the lateral area, the *M. pronator quadratus* could be shown between the radius and the ulna (Fig. 8). The well-developed muscle bundles ran transversally in their direction.

Discussion

The aardvark represents only one living species of the Order Tubulidentata. Many adaptive characters to the fossorial life are morphologically confirmed in this species. Especially the digging apparatus of the aardvark has been completed in the early evolutionary history of the order, since the locomotion and digging mechanisms were established in the fossil species on the Miocene (Patterson 1975). Since the aardvark is also one of the largest recent mammals adapted to digging behavior, we expect that the specific muscular structure may enable the animal to effectively construct the tunnel system.

The strong belly of the *M. pronator quadratus* is noteworthy. In addition, the *M. abductor digiti I longus*

and the *M. pronator teres* are also developed, while the *M. supinator* is distinctive between the humerus and radius. Since the digging behavior requires powerful pronator-supinator mechanism in the forelimb (Kahle et al. 1986), we suggest that the development of the four muscles contribute to the pronator-supinator action of the forearm. In addition, it is noteworthy that some muscles run obliquely in the anterior space of the forearm and induce their tension to rotate the forearm around the ulna shaft. Since the *M. brachioradialis* pulls the medial side of the radius from the humerus, the muscle acts as a powerful supinator of the forearm. In fact the *M. brachioradialis* was named *M. supinator longus* in a classical description (Galton 1868). We also think that the *M. extensor digiti II* may not only function as an extensor of the digits II and III, but also as a supinator of the radius. We suggest that these extensor muscles may support the pronator-supinator movement of the forearm in soil-crushing action.

The extensor muscles can be separated into two groups in their insertion except for the *M. extensor digitorum communis*. The *M. extensor digiti II* and the *M. extensor carpi radialis* insert to the digits-metacarpals II–III, whereas the *M. extensor digitorum lateralis*, and *M. extensor carpi ulnaris* reach the digits-metacarpals IV–V. Although Humphry (1868) pointed out that the *M. extensor carpi radialis* inserted only to the second metacarpals in his material, we have never observed the variation in which the insertion is converted between the III and IV digits-metacarpals. We suggest that the functional role is obviously different between these two digit groups. In fact the distal phalanx and claw are largely developed in the digit II and III, however obviously smaller in the digit IV and V.

In the flexor group, the *M. flexor digitorum superficialis* and the *M. flexor digitorum profundus* inserted all digits-metacarpals. However, the *M. flexor carpi radialis* inserts into the palmer surface of the second metacarpals. Although this muscle is tendinous, its specific insertion to the second metacarpal suggest the strong power of flexion in the digit II. The two heads of the *M. extensor digitorum lateralis* insert to the lateral side of the proximal phalanges IV and V as a strong tendon. These lateral insertions indicate that this muscle does not only extend the lateral two digits but also abducts them. From these data, we think that the crushing of soil is accomplished by the two medial digits and that the lateral two digits mainly act as a remover of the crushed soil in digging behavior. The abducting digits IV and V may not

be effective to crush the soil, but to sweep and throw crushed soil and small stones into its latero-posterior space as a shovel-like structure.

The hind limbs bear the strong crushing power of the forelimbs, when the aardvark digs the ground. The *M. biceps brachii* also contributes to the supinator-pronator movement of the forearm. Since these additional mechanisms supported the digging behavior of the aardvark, the muscles of the brachial region and of the hind limbs should be also functional-morphologically examined in the future.

The digging adaptation has also been completed in the moles. The well-developed *M. supinator* and the *M. pronator teres* act as a main motor of the supinator-pronator movement in digging action of the moles (Hildebrand 1974). The moles simultaneously crush and sweep the soil using the enlarged palm operated by the *Caput humerale* of the *M. flexor digitorum profundus*. The functional separation between the crushing and the sweeping is specialized only in the aardvark, although the supinator-pronator action is also important in digging behavior of both species.

The anatomical nomenclature has not been fixed at least in the forearm muscle in the aardvark. Thewissen and Badoux (1986) named *M. extensor digiti IV* and *V* for the two heads of the *M. extensor digitorum lateralis* in this study. The *M. abductor digiti I longus* in this study was named as *M. extensor ossis metacarpi pollicis* (Galton 1868) or *M. extensor digiti I* (Thewissen and Badoux 1986). The *M. extensor digiti II* in this study corresponds to the *M. extensor digitorum profundus* in the description of Jouffroy (1971).

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