Anatomical variation of habitat related changes in scapular morphology

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SUMMARY

The mammalian forelimb is adapted to different functions including postural, locomotor, feeding, exploratory, grooming and defense. Comparative studies on morphology of the mammalian scapula have been performed in an attempt to establish the functional differences in the use of the forelimb. In this study, a total of 102 scapulae collected from 66 species of animals, representatives of all major taxa from rodents, sirenians, marsupials, pilosa, cetaceans, carnivores, ungulates, primates and apes were analyzed. Parameters measured included scapular length, width, position, thickness, area, angles and index. Structures included supraspinous and infraspinous fossae, scapular spine, glenoid cavity, acromium and coracoid processes. Images were taken using computed tomographic (CT) scanning technology (CT-Aquarium, Toshiba and micro CT- LaTheta, Hotachi, Japan) and measurement values acquired and processed using Avizo computer software and Canvas^{TM} 11 ACD systems. Statistical analysis was performed using Microsoft Excel 2013. Results obtained showed that there were similar morphological characteristics of scapula in mammals with arboreal locomotion and living in forest and mountainous areas but differed from those with leaping and terrestrial locomotion living in open habitat or savannah. The cause for the statistical grouping of the animals signifies presence of the close relationship between habitat and scapular morphology and in a way that corresponds to type of locomotion and speed. The morphological characteristics of the scapula and functional interpretation of the parameters in relation to habitat of each taxon is discussed in detail.

Keywords: Mammalian, Scapula, Morphology, CT analysis

INTRODUCTION

The mammalian scapula is a complex morphological structure formed by ontogenetic fusion of a scapular plate and a coracoid plate (Goodrich, 1986). It is a thin, compact bone that functions as an attachment site for various muscles that connect it with the pectoral girdle and axial skeleton (Ashton and Oxnard, 1963; Larson, 1993). Use of forelimb for various purposes depends on the scapula and hence its morphology is highly variable among species to suit functional demands of the forelimb.

Variations in scapular morphology have developed adaptation to a wide range of locomotor functions from terrestrial pronograde quadrupedalism to highly arboreal suspensory behaviours such as brachiating, hanging and vertical climbing (Young, 2006). Unlike the hind limbs, functions of the forelimbs vary among species. Ungulates forelimbs are specialized for support and movement; that of carnivores have developed claws for catching and pulling a prey while in primates the forelimbs have fingers and nails for carrying food and arboreal suspensory actions. Forelimb functions are therefore considered to play a major role in scapular shape and pattern intraspecific scapular variations.

Several muscles either originate or insert on the scapula, functioning across several joints in the shoulder and upper extremity including the scapulothoracic joint, the glenohumeral joint and the elbow. Thoracoscapular muscles act to stabilize the scapula and provide scapulothoracic motion. These include the trapezius, rhomboideus and serratus ventralis. Flexion of the shoulder joint is accomplished through the coracobrachialis muscle (Provencher *et al.,* 2010). Other muscles with action on the scapula include the teres major, triceps brachii caput longus and biceps brachii. Muscles originating from the scapula have specific site of attachment. These sites include borders, fossae, processes and tubercles and they differ in structural development and complexity from one species to another. Variations of the sites therefore signify the existence of variations in action of the cognate muscles.

Factors causing variations in scapular shape are not fully known. However, several factors have been implicated including the multiple developmental processes acting at different points during ontogeny; intrinsic genetic factors affecting shape and size; epigenetic factors associated with muscle attachment, location, weight, size and utero-neuromuscular activity (Carter *et al,*. 1998; Nowlan and Prendergast, 2005) and environmental factors that cause differential bone growth in areas closest to peak strains generated by patterns of muscle contraction (Herring and Teng, 2000; Zelditch *et al.,* 2004).

The purpose of this study was therefore to examine and compare various scapular features in order to evaluate the relationship of variations in scapular morphology with body size, phylogeny, locomotion and the indigenous habitat of the animals. In this study the computed tomographic (CT) scanning technology (CT-Aquarium, Toshiba, Japan and micro CT- LaTheta, Hotachi, Japan) were used to obtain images and scapula measurements followed by reconstruction of the images using Avizo computer software.

MATERIALS AND METHODS

Computerized tomography (CT) scans

Micro CT-LaTheta, Hotachi, Japan and CT-Aquarium, Toshiba, Japan were used to scan small and large specimens respectively. Images obtained were used to construct images for data acquisition and processing.

Source and preparation of animals

A total of 102 scapulae from 66 species of animals representatives of all major taxa were obtained from various areas in Japan. These include, National Science Museum, Tsukuba, Tokyo; Primate Research Institute, Kyoto University; Ueno Zoological Gardens, Tokyo; Tama Zoological Park, Tokyo; Saitama Children's Zoological garden, Saitama; Yamaguchi and Laboratory animal unit, Yamaguchi University. There were no need for ethical clearance from the Ethical Committee of Yamaguchi University for Animal Protection and Experimentation in Japan because the animals used were dead.

Measurements of scapular parameters

The entire animal forelimb or scapula was scanned to obtain image. All CT-scan images were processed using computer software. Measurements on scapular thickness were generated using the cross section of CT-scan images at maximum width of supraspinous and infraspinous fossae.

Data acquisition and processing

Scapular measurement values were acquired and processed using Avizo version 6.1.1, Maxnet, Japan. Parameters measured include scapular length, width, position, thickness area, and angles. Structures included scapular spine, acromion and coracoids processes. Data on surface area of various parts of scapula such as supraspinous and infraspinous fossae and articular surface of the glenoid cavity were generated using Canvas™ 11 ACD systems, America. Statistical analysis on variance between measurements was performed using Microsoft Excel 2013.

RESULTS

Assessment of scapular morphology from various animals

Mammals exhibit morphological variations in scapular length, width and thickness; being elongated, thin club-stick shaped in rodents; broad width in dolphin species; elongated triangular in ungulates; flat, wide and triangular in carnivores and slender, flat and lever-like shape in primates (Figure 1).

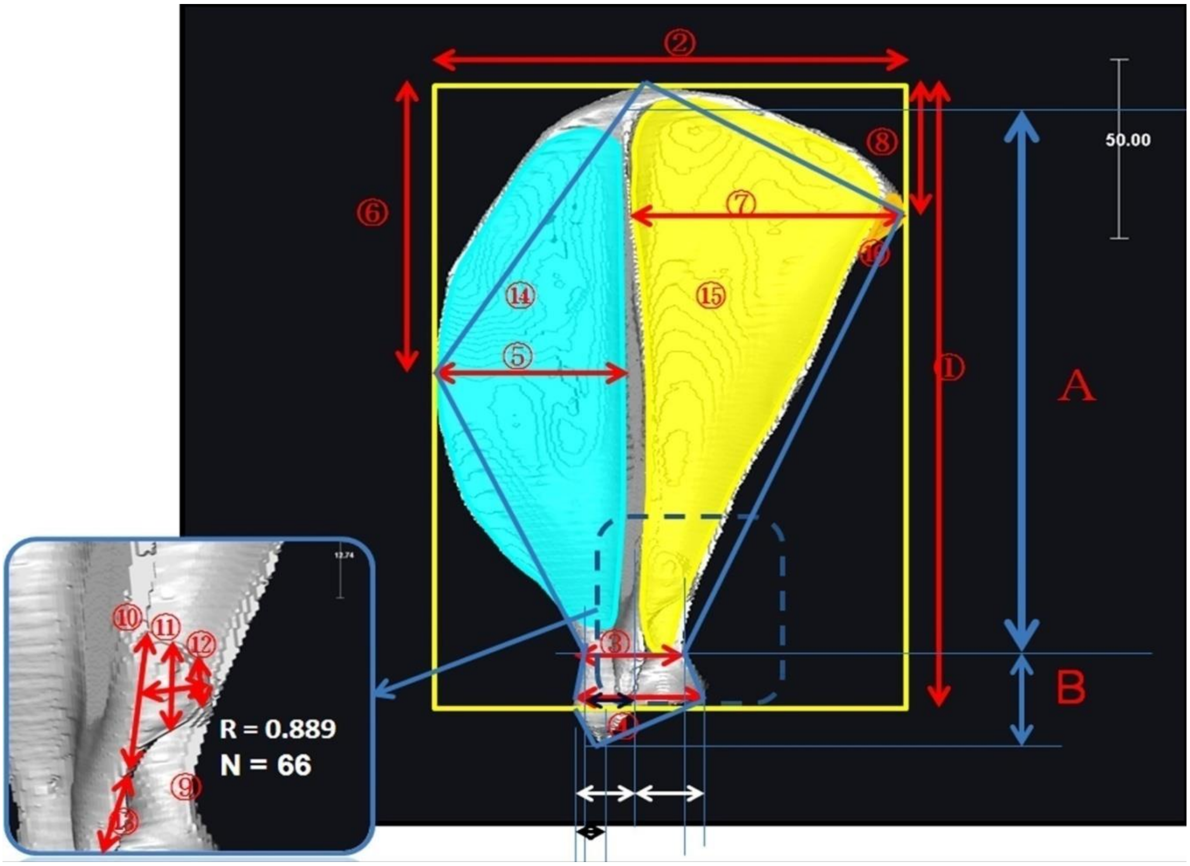

Figure 1A. Numbers representing points used to take measurements of scapula from lateral view. 1, Maximum length; 2, Maximum width; 3, Minimum width; 4, Position of minimum width at distal end; 5, Maximum width of supraspinous fossa; 6, Position of maximum width in supraspinous fossa; 7, Maximum width of infraspinous fossa; 8, Position of maximum width of infraspinous fossa; 9, insert of distal region of scapula; 10, Length of metacromion pocess (greater tubercle) at the base; 11, Width of metacromion pocess (greater tubercle at the body); 12 Length of metacromion pocess (greater tubercle at the apex); 13, Length of acromion; 14, Area of supraspinous fossa; 15, Area of infraspinous fossa; 16, Caudal angle. A, Length of scapula from neck to proximal end; B, Length of scapula from neck to distal end. Scale: 50.0 mm.

Maximum length and maximum width of scapula

Despite the variations is scapular shape, there is no statistically significant difference (length R^2= 0.898; width R^2= 0.85) in maximum length and maximum width amongst scapulae of mammals examined (Figure 2).

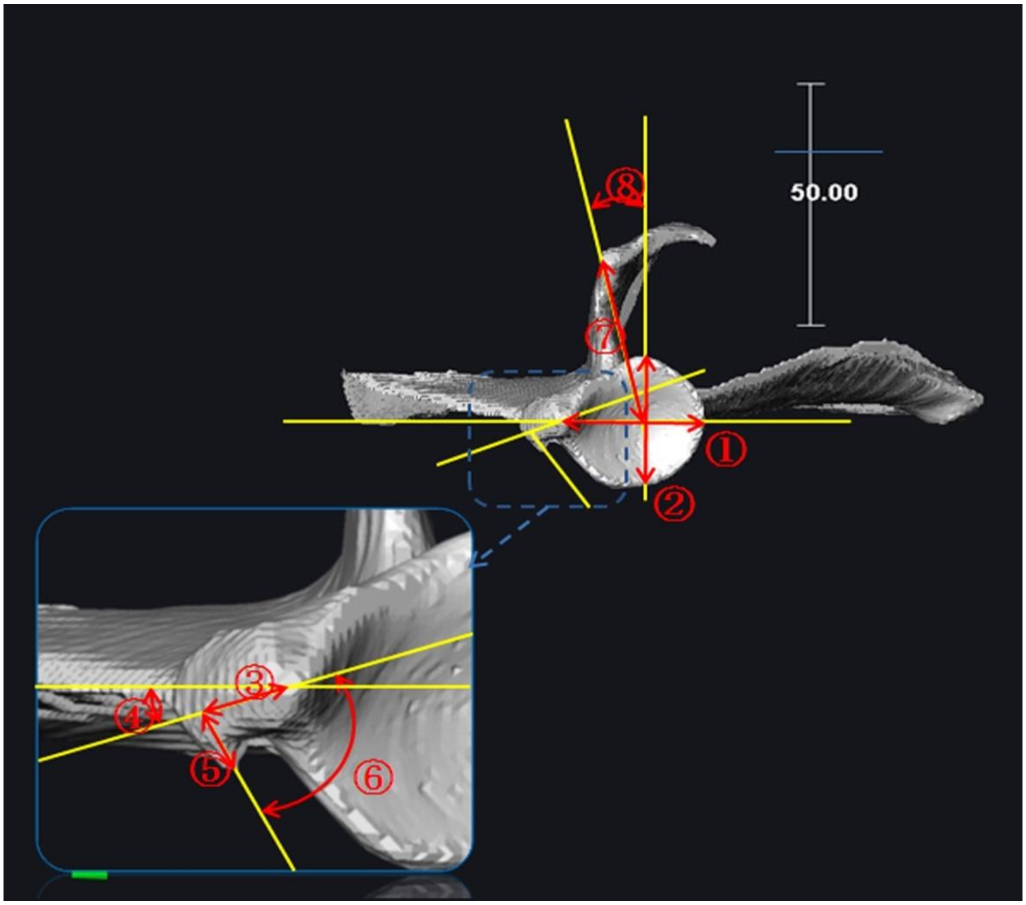

Figure 1B. Numbers representing points used to take measurements of scapula from ventral view. 1, Diameter (cranio-caudal) of glenoid cavity; 2, Diameter (lateral-medial) of glenoid cavity; 3, Length of Supraglenoid tubercle (infra-glenoid tubercle); 4, Angle-alpha, α; 5, Length of coracoid process; 6, Angle-beta, β; 7, Length between center of glenoid and acromion; 8, Angle-gamma, γ. Scale: 50.0 mm.

Ratio of the maximum length and maximum width of scapula

The ratio of the maximum length and maximum width of scapula in primate with terrestrial or leaping locomotion living in open habitat or savannah was higher than that seen in primates with brachiating locomotion living in forest and mountains or highlands. High ratio was also noted in ungulates living in open habitat but lower in those living in mountainous areas (Figure 3).

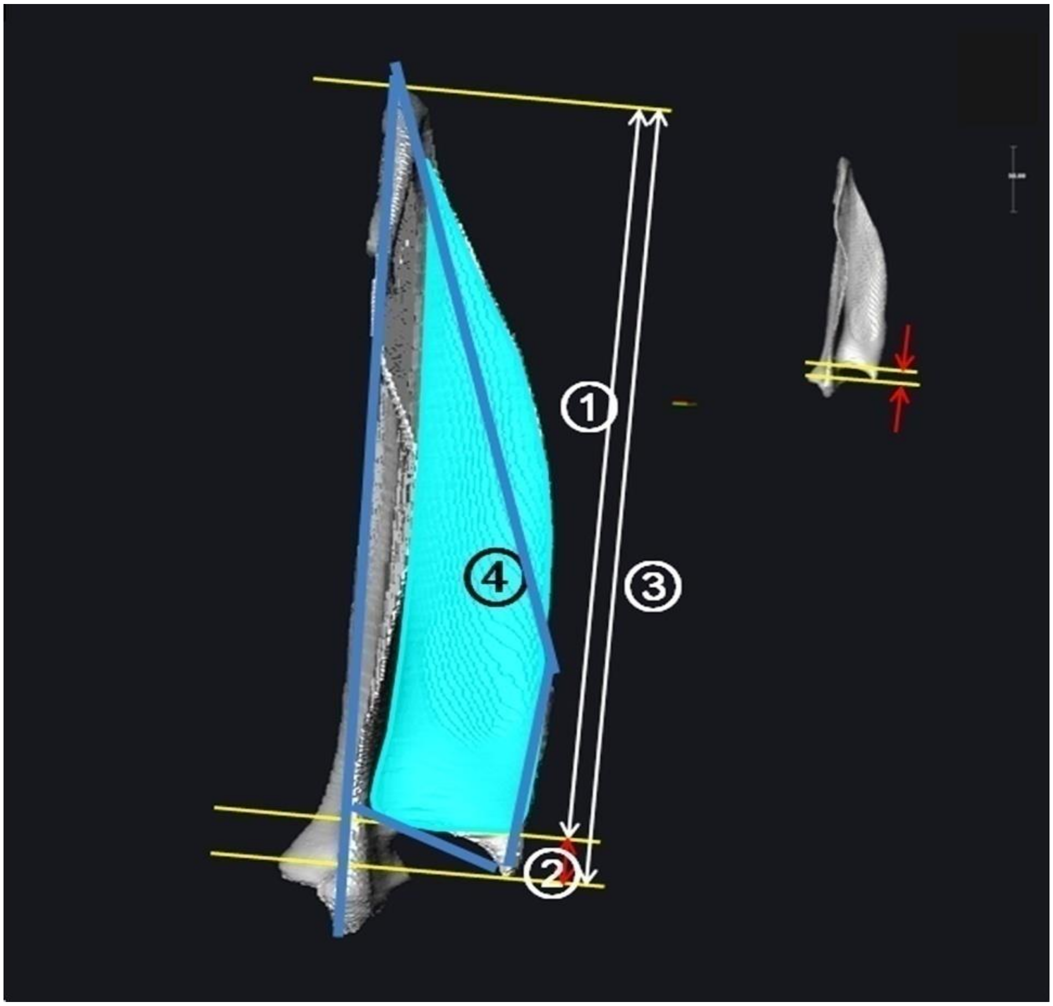

Figure 1C. Numbers representing points used to take measurements of spine of scapula from cranial view and proximal to distal end. 1, Maximum length of spine from neck to proximal end; 2, Maximum length of scapula at neck; 3, Maximum length of spine from proximal to distal end; 4, cranial area of spine of scapula (supraspinous fossa). Scale: 50.0 mm.

Scapular spine characteristics

Position of spine was also found to correlate with an animal of a particular habitat. Proximally positioned spine was seen in primates with arboreal locomotion and ungulates living in mountains and highlands. Distally positioned spine was seen in primates and ungulates living in open habitat or savannah with terrestrial or leaping locomotion (Figure 4). The index of position of scapular spine in ungulates was also different from that of carnivores and rodents. And it was different between primates and carnivores indicating that the locomotory type of an animal is influenced by habitat or environment.

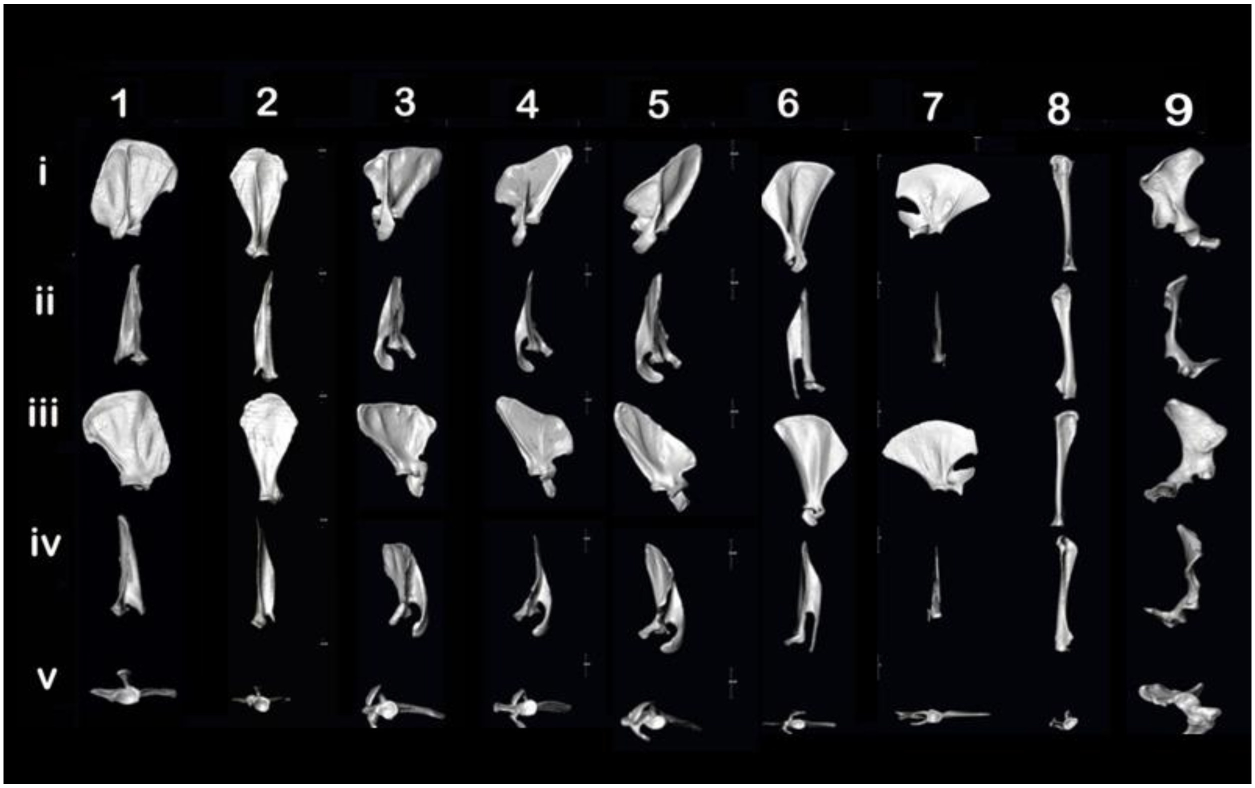

Figure 2. Left scapula of various animals (Columns) presented in five views (Rows) ; (i) lateral, (ii) caudal, (iii) medial, (iv) cranial and (v) ventral. Columns represent (1) Polar bear-Carnivores; (2) Giraffe-Ungulates; (3) Human (4) Baboon-Primate; (5) Chimpanzee- Apes; (6) Rat-Rodents; (7) Dolphin - aquatic habitat; (8) Mole-Diggers and (9) Platypus- Burrows. Scale: 50.0 mm

DISCUSSION

The comparative studies on the morphology of the mammalian scapula have been a focal point to establish functional differences in the use of the forelimb (Roberts, 1974). Scapular features including scapular spine, supraspinous and infraspinous fossae, have been associated with the role of the scapula in locomotion (Inouye and Shea, 1997). In this study, 102 animal scapulae from 66 animal species were assessed and analyzed to obtain measurements and data on comparative scapular morphology. The relationship of the scapular features such as length, width and thickness of supraspinous and infraspinous fossae, position and index of scapular spine, articular surface of the glenoid cavity, acromion and coracoids processes with animal locomotion and habitat was deduced.

Previous studies show that mammals are adapted to diversity locomotor functions in different habitats from terrestrial pronograde quadrupedalism to highly arboreality such as brachiating, hanging and vertical climbing (Young, 2006). Indeed the shape of scapula differs among animals to follow the functions of the forelimb. Differences in scapular length relative to scapular size have also been linked to the variations in thoracic shape and scapular positioning (Taylor, 1997).

In this study, ungulates with heavy body weight were found to have more vertical shaped scapulae with distally positioned maximum length and maximum width relative to the proximal positioned maximum length and maximum in carnivores. Proximally positioned maximum length and maximum width of scapula signifies enhanced stability of the shoulder joint. Increased capabilities for running and jumping on rough grounds in ungulates particularly deer, made possible by the shallow glenoid cavity and help to increase shoulder joint mobility and avoid frequent dislocation. The scapulae of swimmers such as the finless porpoise and long beaked common dolphin are flattened, triangular, with distinct scapular notch. The scapular is elongated in Japanese moles with adaptation for digging while sickle shaped in platypus and short beaked echidna with clawed front paws adapted for pulling out prey and digging to create burrows for shelter. Animals that dig and those with suspensory have distinct differences in scapular shapes, particularly because of the need for developing various structural parts that serve as muscle attachment sites (Lehmann, 1963). Animals with arboreal locomotion elevate the arm above the head using scapular rotation and humeral abduction leading into craniocaudally long and narrow scapulae, more cranially extended supraspinous fossae, more oblique spine and shallow glenoid cavity (Ashton and Oxnard, 1963).

Results obtained in this study also showed that the ratio of the maximum length and maximum width of scapula was high in primate and ungulates with terrestrial locomotion living in open habitat but low in ungulate and primates with brachiating locomotion living in forest and mountains. Position of scapular spine was also found to correlate well with mammals of a particular habitat. Proximally positioned spine was observed in primates with arboreal locomotion and ungulates living in mountains and highlands. Distally positioned spine was seen in primates and ungulates living in open habitat with terrestrial or leaping locomotion. The cause for the statistical grouping of the animals signifies presence of the close relationship between habitat and type of locomotion. Variation in scapular shape may also reflect presence of differences in speed of locomotion amongst animals or involvement of an animal in training and exercise. Influence of habitat on bone morphology has also been shown in previous studies (Janis et al., 2000) in which feeding of ungulates on more abrasive forage was associated with development of craniodental morphology and elongated limbs. However, it has not been successful to show differences in scapular shape between lowland and mountain gorillas using muscle function (Taylor, 1997).

Similarly, the shape of glenoid cavity also varied among animals being circular with small supraglenoid tubercle and without any distinct notch in ungulates but with void shaped glenoid cavity and craniodosaral notch in apes and primates to favour mobile shoulder joint, an adaptation for rapid limb motion. Apes and primates living in mountains and highlands also showed long horizontal length of acromion process but it was short with caudal orientation in relation to the horizontal distance in primates and apes living in open habitat. The acromion process is the site of origin for deltoideus muscle (pars acromialis) which act as a protractor and lateral rotator of humerus (Robert, 1974). A well developed acromion process found in apes living in forest or mountainous areas is therefore linked to arm suspensory and climbing behaviors for improved mechanical leverage for the deltoid muscle. Length of acromion in diggers such as Japanese moles is indicative of force generating from the shoulder musculature.

Likewise the length of coracoid process was long in apes living in forest or mountains but short and rounded in ungulates living in open habitat. The coracoid process projects from medial side of supraglenoid tubercle and forms the site for origin of the coracobrachialis muscle that flexes the shoulder joint, adducts the arm and stabilizes the humeral head within the shoulder joint, particularly during suspensory actions.

In conclusion, this study shows that there is a close relationship between scapular morphology and habitat amongst animals. Variations in scapular shape also reflect existence of differences in speed of locomotion which is enhanced by training and exercise. However, it is worth noting that collecting more data for some taxae with variability in locomotor modes may give additional information on the association of variations in scapular shape with habitat or ecology and type of locomotion.

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REFERENCES

Ashton, H.E., Oxnard, C.E. The musculature of the primate shoulder. *J Zoology,* 29: 553-650. 1963.

Carter DR, Mikic B, Padian K. Epigenetic mechanical factorsin the evolution of long bone epiphyses. *Zool J Linn Soc,* 123: 163–178, 1998.

Goodrich ES. *Studies on the structure and development of vertebrates*. Chicago: Univ Chicago Press. 837 p. 1986.

Larson SG. *Functional morphology of the shoulder in Primates*. *In D. L. Gebo (Ed.) Postcranial adaptation in nonhuman primates* (pp. 45–69). DeKalb: Northern Illinois University Press, 1993.

Lehmann WH. The forelimb architecture of some fossorial rodents. *J Morphol* 113: 59–76, 1963.

Young NM. Function, ontogeny and canalization of shape variance in the primate scapula. *J Anat,* 209: 623–636, 2006.

Nowlan NC, Prendergast PJ. Evolution of mechanoregulation of bone growth will lead to non-optimal bone phenotypes. *J Theor Biol,* 235: 408–418, 2005.

Herring SW, Teng S. Strain in the braincase and its sutures during function. *Am J Phys Anthropol* 11: 575–593, 2000.

Inouye SE, Shea BT. What's your angle? Size-correction and bar-glenoid orientation in "Lucy" (A.L. 288-1). *Int J Primatol* 18: 29–650, 1997.

Janis CM, Damuth J, Theodor JM. Miocene ungulates and terrestrailprimary productivity; where have all the browsers gone? *Proc. Natl. Acad. Sci USA* 97: 7899-7904, 2000.

Provencher MT, Ghodadra N, Romeo AA. Arthscopic management of anterior in instability. Pearls, pitfall and lessons learned. *Orthp Clinic North Am,* 41: 325-337, 2010.

Roberts D. *Structure and function of the primate scapula. In F. A. Jenkins (Ed.), Primate locomotion* (pp. 171–200). New York: Academic Press, 1974.

Taylor AB. Scapula form and biomechanics in gorillas. *J human Evol,* 33: 529–533, 1997.

Zelditch ML, Lundrigan BL, Garland T. Developmental regulation of skull morphology. I. Ontogenetic dynamics of variance. *Evol Dev* 6: 194–206, 2004.