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THE SHOULDER ARCHITECTURE OF BEARS AND OTHER CARNIVORES

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INTRODUCTION

The most characteristic feature of the scapula in bears is the large accessory fossa lying caudad of the infraspinous fossa on the axillary border. This area is separated from the infraspinous fossa by a prominent ridge representing the true axillary border of the shoulder blade. This ridge is sometimes called the inferior scapular spine. The accessory fossa is associated with the origin of a part of the subscapular muscle, and may be known as the postscapular fossa (*Fossa postscapularis*).

The postscapular fossa is an excavation in the lateral surface of the *teres major process*, with which it is not to be confused. The teres major process is a plate-like extension of the axillary border associated with the origin of the teres major muscle, and may be large without any indication of the postscapular fossa (e.g. certain mustelids).

The postscapular fossa is well developed in all bears, regardless of size. It is well formed in a new-born black bear cub, in which the scapula is only 21 mm. long. The fossa is largest in the true bears (*Ursus*) and sloth bear (*Melursus*), and smallest in the polar bear (*Thalarctos*) and the Malayan sun bear (*Helarctos*). It is present, though so reduced as to be inconspicuous, in the Procyonidae; the teres major process is large in all procyonids. The fossa is moderately large in the lesser panda (*Ailurus*), and is present but modified by the greatly expanded infraspinous fossa in the giant panda (*Ailuropoda*). Both the teres major process and the postscapular fossa are wanting in the Canidae and in the cat-like carnivores; in these forms the axillary border near the vertebral angle bears only a more or less prominent scar for the attachment of the teres major muscle (fig. 70).

A most consistent feature of the fossa, regardless of its degree of development, is that it is continued toward the glenoid cavity by a spiral groove that twists around onto the medial side of the blade, where it is continued down to the neck, passing mesad of the infraglenoid tubercle. This rotation amounts to a full 180 degrees (fig. 71).

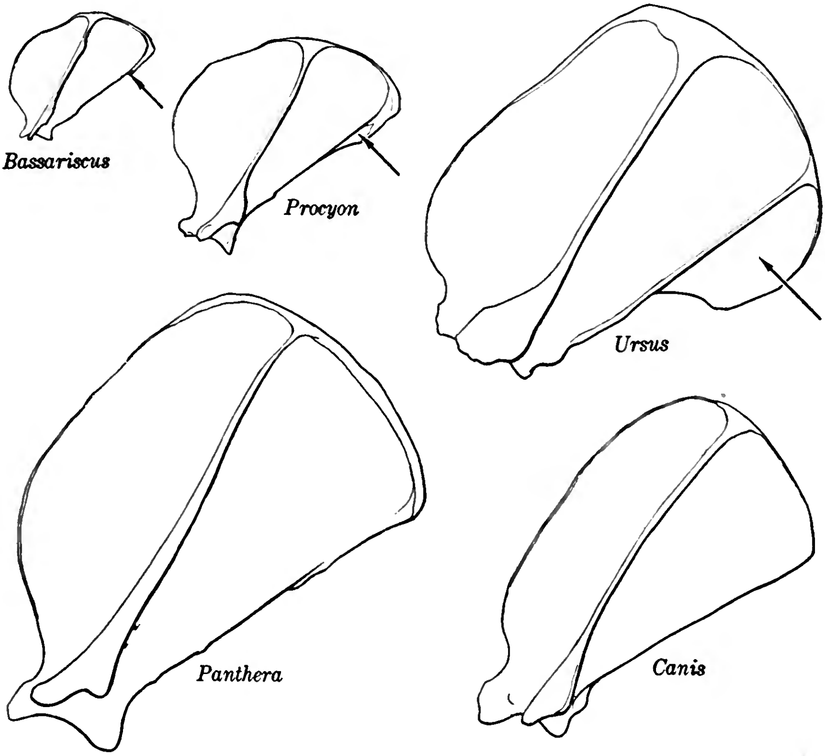

FIG. 70. Lateral view of scapulas of representative carnivores. The arrow points to the postscapular fossa.

The significance of this fossa, so conspicuous that it distinguishes the bear scapula from that of all other carnivores, has been unknown. Work on the closely related giant panda makes it desirable to understand the history and morphological and functional relations of this element. This in turn depends upon knowledge of the muscles associated with the fossa and of the mechanics of the shoulder, both in the bears and in other carnivores.

The bear scapula is rectangular in outline, instead of having the fan shape typical of carnivores. The shape of the bear scapula is due chiefly to the tremendous breadth of the neck, which exceeds the antero-posterior diameter of the glenoid cavity by about one third. The acromion, which provides origin for the acromiodeltoid muscle, is large and plate-like, with a large but relatively indistinct metacromion that functions for the insertion of the levator scapulae

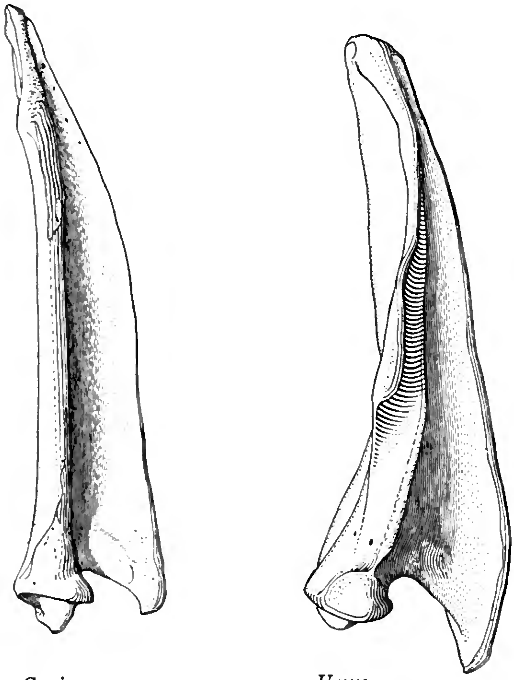

FIG. 71. Glenoid border of scapula of wolf (*Canis lupus*) compared with black bear (*Ursus americanus*) to show the spiral groove leading distad from the postscapular fossa in bears.

ventralis muscle. The acromion projects ventrad beyond the glenoid cavity farther than in any other carnivore.

FLEXOR MUSCLES OF THE SHOULDER IN THE BEAR

The musculature of bears was described by several authors in the nineteenth century—of the black bear (*Ursus americanus*) by Shepherd (1884) and Testut (1890), and of the polar bear (*Thalarctos*) by Kelley (1888). These descriptions are extremely superficial by modern standards, and for illustrations of the limb muscles it is necessary to go back to Cuvier and Laurillard's *Planches de*

Myologie. None of these works contains any clue to the muscles concerned in the postscapular fossa.

Only the flexor muscles of the shoulder are involved in this fossa. I have dissected these muscles on a young black bear (*Ursus ameri-*

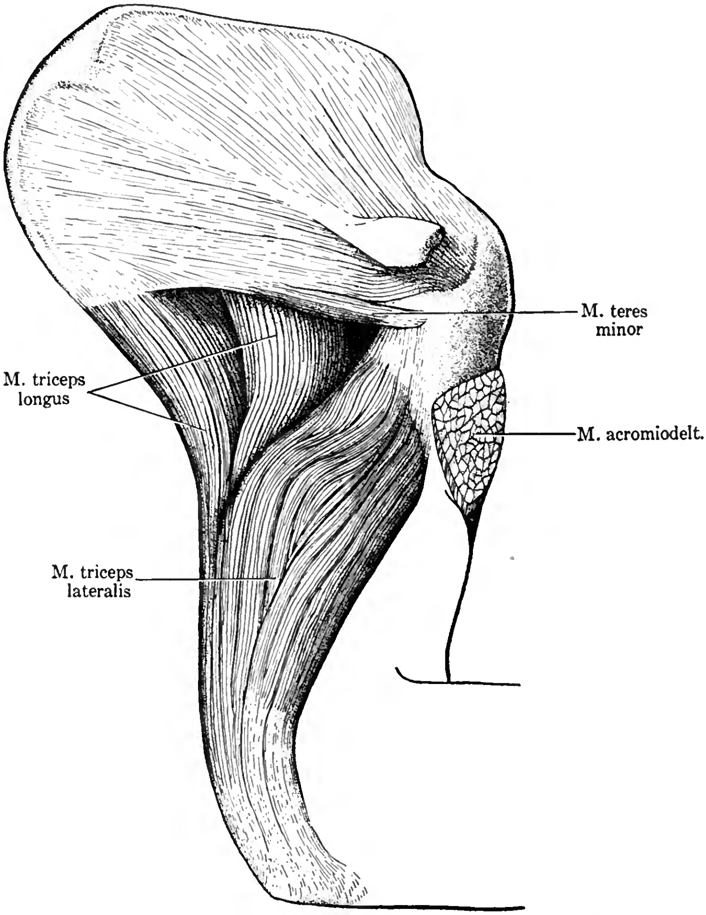

FIG. 72. Lateral view of flexor muscles of shoulder in *Ursus americanus*.

canus), about a quarter grown, born in the zoo of the Chicago Zoological Society.

The triceps is of course chiefly an extensor of the forearm, but, as explained below, the long head—the largest element of the triceps in bears—is an important flexor of the shoulder. It is, moreover, related to the postscapular fossa in bears. In these animals the triceps is powerful, especially the long head. It is divided into the usual three heads: long, lateral, and medial, which have the customary general relations. The long and medial heads are each further divided into two subheads.

M. triceps longus is an extremely large triangular mass lying along the posterior side of the arm, its origin extending along the

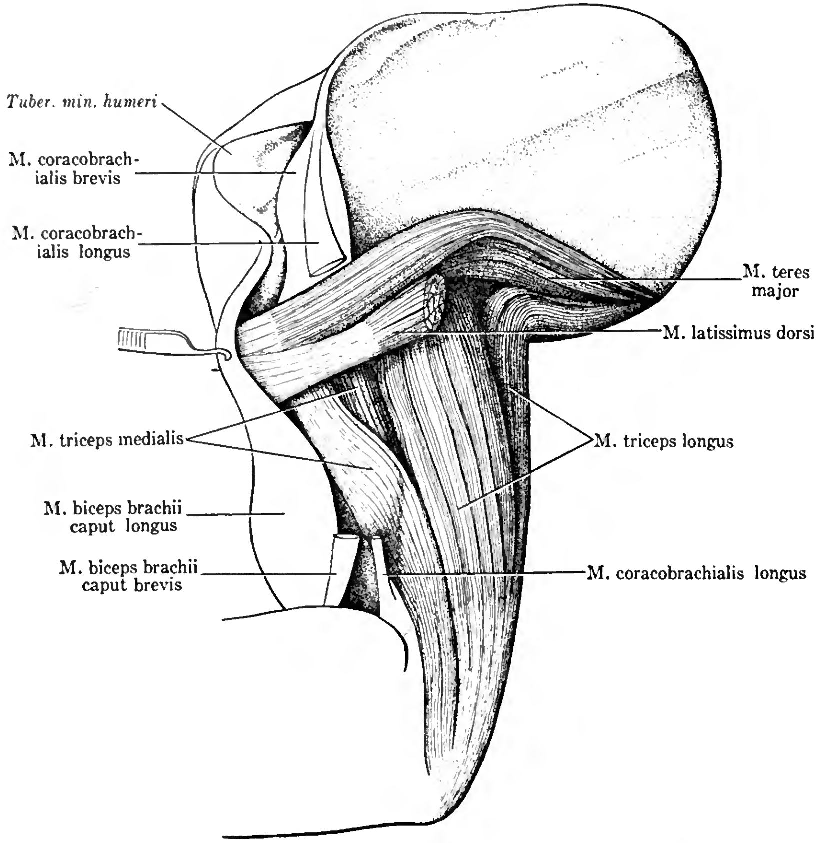

FIG. 73. Medial view of flexor muscles of shoulder in *Ursus americanus*.

whole axillary border of the scapula, from the infraglenoid tubercle to the vertebral angle (figs. 72 and 73). At its origin it is subdivided into anterior and posterior parts, of which the anterior is considerably the larger, but these fuse at about the middle of the arm. Branches of the profunda brachii artery and vein pass out between these two parts. The *anterior* head arises, by fleshy fibers, from the proximal half of the axillary border of the scapula, the line of origin following the prominent crest separating the infraspinatus and postscapular fossae. The *posterior* head continues the line of origin of the anterior head along the crest separating the fossae, but does not attach to bone. Instead it arises from the fascia covering the subscapularis minor lying directly deep to it, and from the fascia covering the infraspinatus and teres major. Origin extends posteriorly to the vertebral border of the scapula. At about the middle of the arm the triceps longus fuses with the lateralis; it remains distinct from the medialis much farther distad.

The remarkable length of the origin of the long triceps, extending the whole length of the axillary border of the scapula, is mentioned by Shepherd and Testut, but not by Kelley; none mentions its subdivision into anterior and posterior parts. In other carnivores the origin of this muscle is restricted to the proximal half or less of the axillary border, except in the giant panda, in which it extends nearly as far as in the bears. The giant panda is also the only other carnivore in which the subdivision into anterior and posterior parts was found.

M. triceps lateralis is a smaller muscle than the longus, running diagonally across the outer surface of the arm (fig. 72). It is intimately united to the triceps medialis on its deep surface throughout most of its length. The lateralis arises almost exclusively from the surface of the brachialis lying immediately beneath it; the surface of the brachialis proximad and anterior to the triceps head is covered with a heavy tendinous aponeurosis. The triceps head reaches bone only in a minute area behind the insertion of the teres minor. In its distal half the lateralis is fused with the adjacent surface of the triceps longus.

M. triceps medialis is composed of a long head and a small intermediate head, separated by the coracobrachialis brevis at their origins but fused below the middle of the arm. The radial nerve and branches of the profunda artery and vein pass through the interval between the two heads at about the middle of the arm. The *long* head is separable from the triceps lateralis only for a very short distance after its origin, which is from a triangular area on the posterior surface of the shaft of the humerus, beginning at the lip of the articular surface, the most superficial fibers arising from the joint capsule. The *intermediate* head takes a tendinous origin from a short line on the postero-medial edge of the shaft of the humerus, immediately beneath and behind the insertion of the latissimus tendon. The triceps medialis inserts, by fleshy fibers, into the medial surface of the olecranon.

M. anconaeus is a flat triangular muscle arising from the triangular area on the posterior side of the distal end of the humerus. It lies deep to the distal part of the triceps. Insertion is into the posterior and lateral sides of the olecranon.

M. teres major is relatively small. It has been displaced completely onto the medial surface of the scapula by the subscapularis

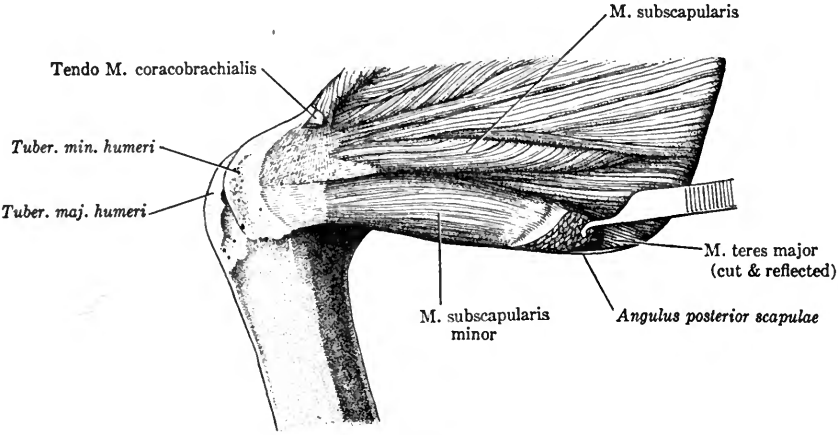

FIG. 74. Medial view of shoulder of *Ursus americanus*, to show M. subscapularis minor.

minor (figs. 73 and 74). The teres major arises almost exclusively from the surface of the subscapularis minor near the vertebral angle of the scapula; it arises from bone only in a narrow line along the axillary edge of the postscapular fossa. The surface of the subscapularis minor from which the teres major takes origin is covered with a heavy tendinous aponeurosis. The teres major terminates in a flat tendon that unites at once with the tendon of the latissimus dorsi and inserts into the roughened scar on the crest of the lesser tubercle at about the juncture of the proximal and middle thirds of the humerus.

M. teres minor is a small but well-defined muscle wedged in between the infraspinatus and the origin of the triceps longus. It arises from a small area on the axillary border of the scapula just proximad of the middle, and from the adjacent border of the infraspinatus. Insertion is by a very short stout tendon into the shaft of the humerus, just below the insertion of the infraspinatus.

M. subscapularis, divided into several tracts by fascial septa, has the usual origin from the deep surface of the scapula. In addition, however, there is a tract of parallel fibers, separated from the main mass of the subscapularis by a fascial septum, along the posterior (axial) border of the scapula where it lies in the spiral groove described above. This is the *M. subscapularis minor* (fig. 74). It has long been known as a variation in man; Frohse and Fränkl (1908) describe it as "a special little muscle that inserts below the lesser tubercle separate from the terminal tendon [of the subscapularis]. It has been given special names by various authors, of which the simplest is the Latin term M. subscapularis minor. It is found regularly in many animals." Haughton (1866b) is the only one who has noticed this muscle in the bear. He lists it under the name "infraspinatus secundus," merely remarking that it "may be regarded as belonging either to subscapularis or to infraspinatus."

In the bear the posterior half of the subscapularis minor is completely covered by the teres major, which takes origin from its surface. It arises from *both* surfaces of the posterior extension of the scapula, on the lateral surface of the bone completely filling the postscapular fossa. The fibers of the subscapularis minor maintain their identity from the subscapularis proper down to their insertion, which is into the ventral part of the subscapularis scar on the minor tubercle. The subscapularis proper inserts into the remainder of this scar, the most dorsal fibers passing over the coracobrachialis tendon to insert into the joint capsule.

The subscapularis proper is innervated by two large subscapular branches that enter the muscle near its insertion. The subscapularis minor is supplied by a separate subscapular branch that, like the branch to the teres major, comes from the axillary nerve.

SHOULDER FLEXORS IN OTHER CARNIVORES

The shoulder flexors were dissected in the following for comparison with *Ursus:*

Canidae	Wolf (*Canis lupus*)
Procyonidae	Cacomistl (*Bassariscus astutus*)
	Coati (*Nasua narica*)
	Raccoon (*Procyon lotor*)
Ursidae	Giant panda (*Ailuropoda melanoleuca*)
Felidae	Domestic cat (*Felis domestica*)
	Lion (*Panthera leo*)

The giant panda is merely an aberrant bear, as I am showing elsewhere (in MS.), and its shoulder muscles are only slightly different from those of other bears.

The closest living relatives of the bears are the Procyonidae. Of the procyonids, *Bassariscus* is remarkably generalized; fossil remains show that it has remained essentially unchanged since the late Miocene. The postscapular fossa is usually wanting in this genus, but often appears as a depression on the lowermost end of the teres major process. It was present in this rudimentary form in three scapulas of eight (four individuals). The long head of the triceps is relatively much smaller than the triceps lateralis, and arises from the lower third of the axillary border of the scapula. The teres major lies along the axillary border, arising chiefly from the teres major process and the adjacent surface of the infraspinatus; fibers also arise from the underlying surface of the subscapularis minor in a line beginning at the teres major process and extending more than half way to the infraglenoid tubercle. The subscapularis minor is about as well differentiated as in the bears but is relatively much smaller. As in the bears, it is innervated by a separate branch coming from the axillary nerve immediately above the origin of the branch to the teres major. Its origin extends onto the lateral surface of the scapula only in those cases in which there is a rudimentary postscapular fossa. At its insertion the fibers of the subscapularis minor pass superficial to the posteriormost fibers of the subscapularis proper, and insert into the lower part of the subscapularis scar on the lesser tubercle.

In summary, the shoulder flexors of *Bassariscus* differ from the generalized carnivore condition in several features that foreshadow conditions in the bears. The teres major process is relatively large and plate-like, and the subscapularis minor sometimes encroaches slightly onto its lateral surface, producing a rudimentary postscapular fossa. The spiral groove lying along the axillary border of the scapula in other procyonids and bears is scarcely indicated, however. At its insertion the subscapularis minor crosses over the posteriormost fibers of the subscapularis proper. The subscapularis minor is innervated by a separate branch coming from the axillary nerve.

In *Nasua* and *Procyon* the shoulder architecture is fundamentally as in *Bassariscus*, but slightly more advanced in the direction of the bears. The postscapular fossa is typically, instead of sometimes, present, and is continued into a well-defined spiral groove along the axillary border of the scapula. The subscapularis minor is similar to that of *Bassariscus*. The teres major lies in the usual position along the axillary border of the scapula, at its origin embracing the subscapularis minor like a U. The triceps longus is relatively much larger than in *Bassariscus*, but is composed of a single head that arises from the ventral one-fourth to one-third of the axillary border of the scapula.

In the dogs and cats the shoulder flexors are somewhat different from those in the procyonids and bears. These differences, though slight, are important to an understanding of the extremely specialized conditions in the bears. They highlight the importance of the seemingly slight departures from the generalized architecture found in the Procyonidae.

In *Canis* the spiral groove is indicated on the axillary border of the scapula, but there is no teres major process and the "groove" (which becomes convex toward the vertebral angle) ends abruptly at the teres major scar. In *Felis* and *Panthera* (and the still more primitive civets) there is no spiral groove and no teres major process. In both dogs and cats the posteriormost tract of the subscapularis (the subscapularis minor) is not clearly differentiated from the remainder of the subscapularis. This is particularly evident at the insertion, where the "minor" tract fails to maintain its identity. In the dog the "minor" tract is composed of parallel fibers as in the procyonids and bears, but this is not true in the cats, in which it is more complex. This tract is innervated by twigs from the subscapular nerves supplying the remainder of the subscapularis, not by a special branch coming from the axillary nerve. The teres major arises chiefly from the scar on the axillary border near the vertebral angle, but takes accessory origin from the underlying surface of the subscapularis and from the infraspinatus. Among the forms dissected, origin of the long triceps is from the ventral half or less of the axillary border, except in the lion.

In the lion the triceps longus differs sharply from that of the domestic cat, and is remarkable for its similarity to the longus of the bears. In the lion this is by far the most powerful element of the triceps complex. Its line of origin is longer than in the cat, extending from immediately above the glenoid cavity to the level of the teres major scar, more than half way to the vertebral angle. Immediately behind this main head is a much smaller accessory head (the dorso-epitrochlearis externus of Scharlau), a tongue-like muscle arising from the heavy fascia over the infraspinatus. The edge of the accessory head is within 60 mm. of the vertebral angle of the scapula. It fuses with the main head at about the middle of the arm. Thus in the lion, as in the bear, the line of origin of the longus is extended toward the vertebral angle, and in both this is accompanied by a secondary splitting of the muscle.

MECHANICS OF THE SHOULDER IN CARNIVORES

Unfortunately, the considerable knowledge of the architecture and functioning of the shoulder in man has little application to tetrapods because of the very different mechanical relations. Act-

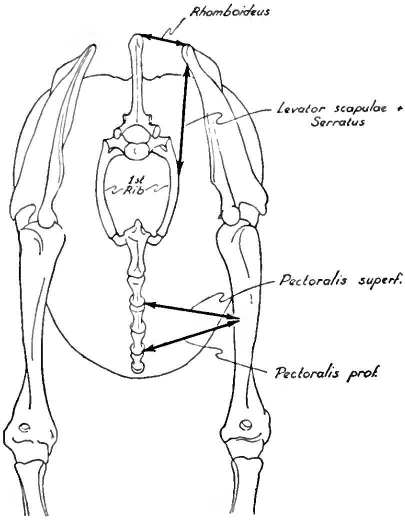

FIG. 75. Directions of pull of muscles tying fore limb to body in the dog (anterior view).

ually, with the scapula lying in the same plane as the limb, and the limb used for support and propulsion rather than prehension, conditions are far simpler in tetrapods than in man. Ellenberger and Baum (1943) have summarized the actions of limb muscles in the horse, and Gray (1944) has presented an extensive review of the mechanics of the tetrapod skeleton, with special emphasis on the limbs and locomotion. Neither of these is precisely what is required here, but both have been drawn upon freely.

The tetrapod shoulder functions in three ways: (1) to transmit the weight of the body to the limb; (2) as the proximal end of an extensible strut (represented by the limb as a whole) operated by the *extrinsic* muscles acting between limb and body; and (3) as a part of a lever system operated by the *intrinsic* muscles of the limb.

A certain muscle group is related to each of these functions, with some muscles participating in more than one.

Load Transmission.—In quadrupedal mammals the weight of the anterior part of the body is transmitted to the limb almost exclusively by the levator scapulae and serratus muscles, which form a continuous sheet in carnivores, extending from the upper edge of the scapula to the anterior ribs and posterior cervicals. Thus the thorax is suspended in a muscular sling (fig. 75). The pectoralis profundus forms a similar, though much less effective, ventral sling. The *center of rotation* of the scapula, in both the transverse and sagittal planes, is the vertebral border of the scapula: the point of attachment of the levator scapulae-serratus. Rotation around this center in the transverse plane (adduction and abduction of the limb) is checked by the rhomboids above the center and the pectorals below, assisted by the lateral extrinsic muscles (especially the trapezius) and fascia, which strap the shoulder down to the thorax. *Load transmission from trunk to limb is effected chiefly by the medial extrinsic muscles of the shoulder.*

Strut System.—As Gray has pointed out, the limb as a whole moving around its center of rotation may be regarded as a strut. Forces moving the limb as a whole can be exercised only by muscles arising from the body and therefore extrinsic to the limb. In the shoulder these muscles are chiefly lateral to the limb bones (fig. 76). They are arranged in two systems lying on opposite sides of the long axis of the limb. The common resultant of their combined forces is an upward thrust along the axis of the limb. *As a group the lateral extrinsic muscles oppose the action of the medial extrinsic muscles.* This action supports the weight of the limb during the recovery phase of the stride. For the cephalohumeral and latissimus dorsi this is a secondary function; they are primarily an extensor and a flexor, respectively, of the shoulder joint.

Lever Systems.—The limb is a system of levers, which are operated chiefly by muscles *intrinsic* to the limb, i.e. by muscles that arise as well as insert on the limb bones themselves. In the scapulohumeral articulation six types of movement are possible: *anteroposterior axis,* (1) extension and (2) flexion; *transverse axis,* (3) abduction and (4) adduction; *rotation around limb axis,* (5) supination and (6) pronation. Extrinsic muscles participate in four of these movements: extension (cephalohumeral), flexion (latissimus), adduction (pectorals), and pronation (latissimus).

Rotatory movements of the fore limb are limited in carnivores, though not so limited as in ungulates. Photographs show lions with the fore paw lying palm upward, and bears in comparable positions of supination. I can find no evidence of pronatory ability (which in man at least takes place in the shoulder rather than the

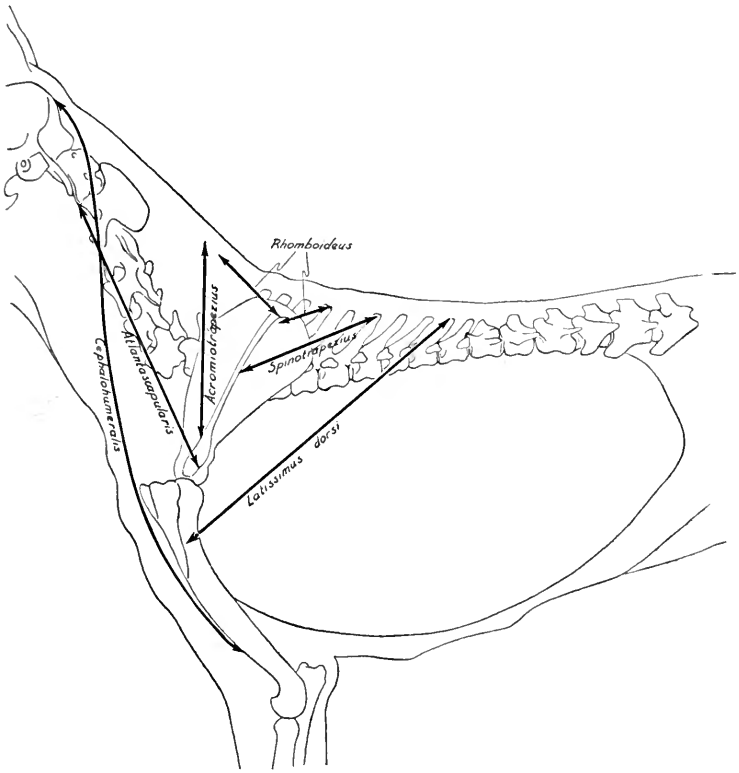

FIG. 76. Directions of pull of muscles tying fore limb to body in the dog (lateral view).

elbow) in these animals, although several muscles, to judge from their topographic relations, are capable of producing pronation.

Movements of abduction and adduction are also limited in carnivores. The vertically compressed thorax prevents extensive adduction, though the pectorals are powerful and mechanically very favorably situated. It has been stated (e.g. Baum and Zietzschmann) that movements of abduction and adduction are limited in the dog by the tendons of the supra- and infraspinatus and subscapularis, which are said to act as lateral ligaments of the shoulder joint. This is not true; the origins of these muscles on the scapula do not extend down to the articulation, and consequently the distal ends bridge over much longer gaps than do lateral ligaments and include muscle as well as tendon fibers. Moreover, on a living dog or cat the humerus can be forcibly abducted to a horizontal position

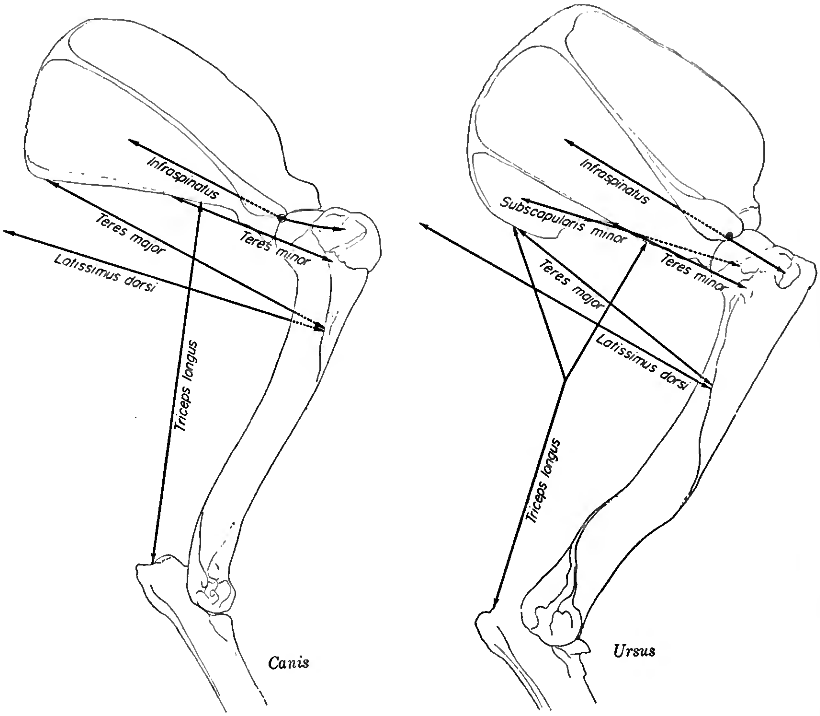

FIG. 77. Directions of pull of flexors of shoulder in the bear compared with the dog. The small circle represents the approximate center of rotation of the shoulder joint.

and it is obviously the *pectoral muscles* that limit further abduction, as can readily be determined by simple palpation.

Fixation of Shoulder.—The scapula, unlike the pelvis, does not offer an immovable point of origin for muscles operating between the scapula and humerus, and the glenohumeral articulation is notably free in mammals. The head of the humerus is held in place much more by muscles than by ligaments or bony processes.

It appears that *in carnivores many of the short powerful scapular muscles are far more important in fixing the joint than in producing movement,* contrary to statements that have been made in the literature. This is particularly true of powerful muscles, like the infraspinatus or subscapularis, that are in a mechanically unfavorable position to operate levers, and whose possible lever actions are far more effectively carried out by other muscles. An attempt was made to demonstrate the actions of such muscles on a crude model. The scapula and humerus of a black bear were taped together loosely with adhesive tape, and strings run through screw-eyes or holes drilled through the bones along lines corresponding to the directions of force of individual muscles. From this it is evident that the actions of many of these muscles as given by Ellenberger and Baum or by Reighard and Jennings are either impossible or of minor importance.

Two sets of muscles are important in fixation of the shoulder: those strapping the scapula down to the thorax, and those fixing the glenohumeral articulation. Muscles acting chiefly to strap down the scapula are the rhomboids, spinotrapezius, and acromiotrapezius. Those acting chiefly to fix the shoulder joint are the supraspinatus, infraspinatus, and subscapularis. Naturally all other shoulder muscles may contribute to fixation of the shoulder, but this appears to be the *chief* function of those just enumerated.

Table 1 represents an attempt to classify the muscles acting on the axes of the shoulder joint in carnivores. Actions have been determined on the basis of direction of pull, verified where necessary by experimentation as described above. Unfortunately this admittedly unsatisfactory method is the only one presently available. The table is modeled after Grant (1942, Morris' *Human Anatomy*, ed. 10, p. 570). It will be noted that the actions presented here differ considerably from those given by Howell (1926, *Anatomy of the Wood Rat*, p. 185).

TABLE 1. MUSCLES ACTING AT THE SHOULDER JOINT IN CARNIVORES

(A) *Longitudinal axis—abduction and adduction*

Abduction:	Adduction:
Spinodeltoid	Pectoralis superficialis
Acromiodeltoid	Pectoralis profundus
	Coracobrachialis longus and brevis

(B) *Transverse axis—extension and flexion*

Extension:	Flexion:
Cephalohumeralis	Latissimus dorsi
Supraspinatus	Teres major
(Biceps)	Triceps longus
(Coracobrachialis longus)	Spinodeltoideus
	(Acromiodeltoideus)
	(Pectoralis profundus posterior)

(C) *Humeral axis—lateral and medial rotation*

Lateral rotation (supinatory):	Medial rotation (pronatory):
Infraspinatus	Subscapularis
Teres minor	Latissimus dorsi
Spinodeltoideus	Teres major
	Pectoralis superficialis
	Pectoralis profundus
	(Cephalohumeralis)

(D) *Support*

Levator scapulae and serratus
Pectoralis profundus anterior

(E) *Fixation*

Of scapula:	Of shoulder joint:
Rhomboideus	Supraspinatus
Spinotrapezius	Infraspinatus
Acromiotrapezius	Subscapularis
Levator scapulae ventralis	(also all other shoulder muscles)

Table 2, compiled from figures given by Haughton, gives the relative weights (expressed as percentages) of the shoulder and arm muscles of the domestic dog, a black bear, and large cats. The material used is, of course, inadequate for accurate work, but it has the considerable advantage that the observations were all made by a single person. These figures reveal rather surprising uniformity, in view of the dissimilarities among the dogs, bears, and cats in habits and body form. In only a few instances does one form vary from the others by as much as 3 per cent. The dog is notable only for the size of the elbow extensors (triceps), and this agrees with available figures for the horse (Schauder, 1924), indicating that enlargement of this muscle group is associated with cursorial locomotion. In the bear the scapular mass is larger than in either the dogs or cats, but none of the other muscle groups shows any notable deviations. In the large cats the shoulder adductors (pectorals) are relatively enormous, while the elbow extensors (triceps) are very small.

ORIGIN OF THE SHOULDER ARCHITECTURE OF BEARS

The most distinctive features in the shoulder architecture of bears, in comparison with other carnivores, are:

1. Broad scapula, especially immediately above glenoid cavity
2. Large postscapular fossa
3. Large subscapularis minor muscle
4. Heavy scapular musculature
5. Prominent, ventrally projecting acromion
6. Extensive origin of triceps longus muscle

TABLE 2. RELATIVE WEIGHTS OF SHOULDER AND ARM MUSCLES IN CARNIVORES
(Based on Haughton's figures)

	Canis[1]		*Ursus*[2]		*Panthera*[3]	
Scapular:						
Spinotrapezius, Acromiotrapezius	3.6		7.1		3.0	
Levator scapulae ventralis	2.3		3.4		1.3	
Levator scapulae dorsalis + serratus	11.8		11.0		8.8	
Rhomboideus	4.1		3.9[4]		4.1	
Infraspinatus	5.6		4.0		5.3	
Subscapularis	4.7		6.1		6.0	
Total Scapular		32.1		35.5		28.5
Shoulder Extensors:						
Cephalohumeralis	6.0		7.6		9.2	
Supraspinatus	7.2		4.4		6.8	
Total Shoulder Extensors		13.2		12.0		16.0
Shoulder Flexors:						
Latissimus dorsi	10.3		9.7		10.3	
Teres major	2.8		2.0		3.8	
Teres minor	0.4		0.3		0.3	
Total Shoulder Flexors		13.5		12.0		14.4
Shoulder Abductors:						
Spinodeltoid, Acromiodeltoid	2.7		3.5		1.2	
Total Shoulder Abductors		2.7		3.5		1.2
Shoulder Adductors:						
Pectorales	14.0		13.1		22.3	
Coracobrachialis	0.3		0.8		0.1	
Total Shoulder Adductors		14.3		13.9		22.4
Elbow Extensors:						
Triceps	20.6		16.9		12.1	
Total Elbow Extensors		20.6		16.9		12.1
Elbow Flexors:						
Biceps	2.2		3.7		3.6	
Brachialis	1.3		2.6		1.6	
Total Elbow Flexors		3.5		6.3		5.2
Total		99.9		100.1		99.8

[1] Means for two Irish terriers.

[2] Weights from one adult female "Virginian bear" [=*Ursus americanus*].

[3] Means from one lion, one lioness, and one tiger.

[4] Weight estimated. No figure given by Haughton.

None of these differences is absolute; each is merely a quantitative difference from the normal carnivore condition. There is nothing qualitatively new in the shoulder of the bear.

A mechanism as complex as the shoulder defies mechanical analysis, and it is hopeless to attempt to compare the relative efficiency, for a particular type of movement, of the bear's shoulder with that of any other carnivore. Often a far more effective technic is the method of analogy, wherein similar or identical mechanical problems have been solved in an unrelated animal. Comparison of such an animal with the animal under consideration may reveal morphological convergences resulting from similar mechanical factors too subtle or too complex for analysis. Problems of function and design are thus studied at second-hand, so to speak.

Examination of the shoulder architecture of the giant anteater (*Myrmecophaga*) reveals that it is strikingly convergent with that of *Ursus*. Each of the six points enumerated above also characterizes the anteater, and in each except (6) the condition is more exaggerated than in *Ursus;* origin of the triceps longus is extensive, but it is not continued to the gleno-vertebral angle as in the bears. The post-scapular fossa and subscapularis minor muscle, in particular, are enormous in *Myrmecophaga*. Now, the whole fore limb in this animal is adapted to tearing termite hills apart. The chief movement involved in such behavior is retracting the fore limb against considerable resistance, which involves forces not associated with normal locomotion. The most important of these is a pull along the longitudinal axis of the limb (the reverse of the *thrust* involved in weight bearing) that would tend to depress the scapula ventrad and anteriorly and to dislocate the head of the humerus from the shallow glenoid cavity. These tendencies would be counteracted chiefly by the lateral extrinsic muscles of the shoulder (trapezius, levator scapulae ventralis) and the muscles that fix the shoulder joint (supraspinatus, infraspinatus, and subscapularis), respectively. On the lateral side of the joint these are assisted by other muscles, notably the deltoids, *but on the medial side the subscapularis is the only muscle that fixes the joint.* This, I believe, is the reason for the enlargement of the subscapularis, which is achieved by enlargement of the subscapularis minor because the subscapularis proper already occupies all the medial surface of the scapula.

Bears, of course, are not burrowers or powerful diggers, but they are active and skillful climbers. The peculiar measuringworm-like technic used in climbing vertical tree trunks has been called "bracing" or "prop" climbing (*Stemmklettern*) by Hans Böker. The portion of the body weight not supported by the hind legs is suspended from the fore legs. The forces acting on the fore limb would then be the same as in the digging of the anteater, except that the position of the load is reversed.

It is interesting that bears are on the threshold of physical inability to climb, because of the increasingly unfavorable ratio of mass (which increases as the cube) to muscle cross section (which increases as the square) of linear dimensions. The little black bear is an active and persistent climber. The larger European brown bear is said by Brehm to climb skillfully, except when it becomes large and heavy. Seton says that the still larger grizzly never climbs as an adult, although grizzly cubs "commonly and readily" do. The huge Alaskan brown bear is not known to climb. Thus 200 to 300 pounds is the maximum weight that a bear is able to hoist up a vertical tree trunk.

The shoulder architecture of bears is designed to resist pulling forces along the long axis of the limb, the reverse of the thrust associated with normal tetrapod locomotion.

From the phylogenetic standpoint, all the features characterizing the shoulder architecture in *Ursus* are wanting in generalized carnivores, but exist in rudimentary form in the primitive procyonid *Bassariscus*. They are further specialized in the bear direction in *Procyon* and *Nasua*. Cacomistls are excellent and agile climbers, and raccoons and coatis are, of course, extremely arboreal. Now, a cacomistl weighs only about two pounds, and an adult raccoon from 15 to 18 pounds, while a black bear scales from 200 to 300 pounds. Thus the degree of development of the postscapular fossa is directly correlated with the size of the animal. The bears have reached—most species have exceeded—the weight limit below which "bracing climbing" is mechanically possible. The powerful shoulder architecture, particularly the large postscapular fossa, reflects the increasingly unfavorable relation between mass and area of cross section that is associated with increased size of organism. The enlarged postscapular fossa, or at least the subscapularis minor with which it is associated, is not merely a secondary postnatal adjustment, however. That it has a definite genetic basis is shown by a new-born black bear cub, which would have weighed scarcely more than half a pound, in which the fossa is relatively as large as in the adult.

Morphologically similar conditions have been evolved independently in the anteaters and armadillos in connection with the similar mechanical demands of digging. It is remarkable that the burrowing carnivores (the badgers and their relatives) have failed to develop a similar shoulder architecture.

The shoulder architecture of *Bassariscus* is slightly differentiated in the bear direction, and it is tempting to speculate that this represents the initial minor recasting of the carnivore shoulder architecture that determined, at this primitive level, the future architecture of the bears. This may be true, but the data are not adequate to prove it. Under any circumstances, however, *the shoulder architecture of bears is, morphologically, an exaggeration of the features characterizing the shoulder architecture of procyonids.*

SUMMARY AND CONCLUSIONS

1. In carnivores, load transmission from trunk to fore limb is effected chiefly by the medial extrinsic muscles of the shoulder.

2. As a group the lateral extrinsic muscles of the shoulder oppose the action of the medial extrinsic muscles.

3. The lever system of the fore limb is operated chiefly by the intrinsic limb muscles.

4. In carnivores many of the short powerful scapular muscles are far more important in fixing the joint than in producing movement.

5. The shoulder architecture of bears is designed to resist pulling forces along the long axis of the limb, the reverse of the thrust associated with normal tetrapod locomotion.

6. The shoulder architecture of bears is, morphologically, an exaggeration of the features characterizing the shoulder architecture of procyonids.

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