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ABSTRACT

The first reports on *Deinonychus antirrhopus* Ostrom tentatively identified a solitary, incomplete bone from the Yale Quarry near Bridger, Montana, as a right pubis. Subsequent examination and comparison with remains of other taxa have established that bone to be a right coracoid of surprisingly large size. The element is redescribed here with a corrected reconstruction of the pectoral girdle and a revised interpretation of the relevant pectoral musculature and functions. The unusually large size of the coracoid is believed to be related to enlarged pectoral muscles that were important in some predatory activities.

Introduction

During the course of my original analysis of the *Deinonychus* remains recovered from the Yale Quarry near Bridger, Montana (Ostrom, 1969a,b), one incomplete element was described which I was unable to identify with certainty. Its general configuration was that of a coracoid, but upon comparison with the scapulocoracoids of other theropods, that identification was discarded because the bone in question was two to three times larger than expected for the known scapulae of *Deinonychus*. Nor did this bone compare well with the coracoid (or any other element) of *Tenontosaurus*, the only other taxon recovered from the Yale *Deinonychus* Quarry. Finally, with some reservations, I identified this bone as a pubis, chiefly because it was found in close association with a right ischium (see fig. 65A, Ostrom, 1969b) in the Yale Quarry.

Peter Whybrow, now at the British Museum (Natural History), while in the process of constructing a free-mount of *Deinonychus* (now being completed by P. Chatrath), concluded that my tentative identification could not be correct. Further comparisons with additional theropod material and re-examination of the scapulae of *Deinonychus* (AMNH 3015) have established to my satisfaction that this element actually is a right coracoid, although of unusual shape and extraordinary size.

In addition to the obvious need to correct the previous error, it also seems worthwhile to re-examine the morphology and function of the pectoral arch and forelimb in the light of this new information.

Abbreviations

Institution names have been abbreviated as follows:

AMNH American Museum of Natural History, New York City
BS   Bayerische Staatssammlung, Munich
GIMAS Geological Institute, Academy of Sciences of the Mongolian People's Republic, Ulan Bator
YPM   Yale Peabody Museum of Natural History

Description

Preserved with the left scapula (AMNH 3015) of *Deinonychus* is the glenoid portion of the coracoid. Although imperfectly preserved, this fragment
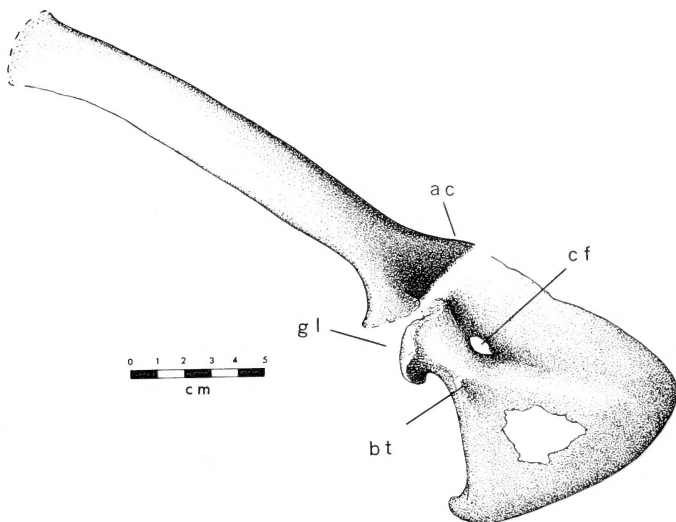
FIG. 1. Right scapulocoracoid of *Deinonychus antirrhopus* as reconstructed from separate elements. The scapula (AMNH 3015) is from the American Museum Quarry (see Ostrom, 1969b, fig. 1A); the coracoid (YPM 5236) was recovered from the Yale Quarry (Ostrom, 1969b, fig. 1B). Although the coracoid seems disproportionately large, the two bones appear to have come from equivalent-sized individuals, judging from the respective dimensions of elements in common from both sites, (see tables 7-11, Ostrom, 1969b). Abbreviations: *ac* = acromial (deltoid) process; *bt* = biceps tubercle; *cf* = supracoracoid foramen; *gl* = glenoid. The scapula and coracoid are illustrated in the same plane, hence the coracoid is viewed in anterolateral aspect, rather than lateral.

corresponds closely in size and morphology with the corresponding region of the present bone (YPM 5236) and confirms the present identification.

The coracoid is roughly triangular in outline (the upper part adjacent to the scapular suture is missing), moderately convexo-concave (externally-internally), and bears a very prominent anterolateral projection immediately anterior to the glenoid rim. Walker (1972) has termed a similar coracoid prominence in *Sphenosuchus* (traditionally classified as a thecodont, but currently considered a crocodilomorph by Walker) the "biceps tubercle." Osmolska *et al* (1972) noted a comparable feature in the theropod *Gallimimus* and labeled it the "coracoid tuber." The supracoracoid foramen is situated immediately dorsoanteriorly to this coracoid prominence, at the bottom of a broad depression. Its passage through the coracoid from within is clearly in a forward direction.

The glenoid moiety and the adjacent region that articulated with the scapula are the most robust portions. The preserved part of the scapular articulation is nearly circular in outline and is strongly digitate. A stout column, nearly circular in section, extends ventroanteriorly from the glenoid-scapular region to the coracoid tuber (or biceps tubercle), then veers ventrally along the posterior margin with diminishing robustness, and finally disappearing in a caudally-directed hook-like flange at the lower coracoid extremity. The posterior margin between the glenoid rim and the ventral "hook" is the most robust of all free coracoid margins. The inferior margin is moderately thick but is not expanded, and the upper anterior margin is thin-edged throughout. Presumably, this latter edge thickened near its junction with the scapula, because the left scapula (AMNH 3015) bears a thick acromial or deltoid border.

Internally, a sharp concavity occurs at the site of the coracoid tuber (beneath it), delineated above and below by bony struts or thickenings extending forward. Anteriorly, this concavity apparently was floored by extremely thin bone (now lost) or perhaps was fenestrated.

As illustrated in Figure 2, the coracoid of *Deinonychus*, compared with that of various other theropods, is much longer (relative to scapular length) and much deeper (dorsoventrally). Its anteroposterior dimension is 107 mm (approximately 60% of scapular length), compared with a vertical dimension that exceeded 100 mm. In addition, the coracoid tuber or biceps tubercle is much more prominently developed than in any other theropod of which I am aware. I have not had the opportunity to check a wide variety of theropod coracoids, but it appears that a correlation may exist between tuber prominence and relative forelimb length. *Gorgosaurus, Albertosaurus* and *Tyrannosaurus* (with reduced forelimbs) have little or no tuber development, whereas *Allosaurus, Struthiomimus* and *Gallimimus* all have distinct coracoid tubers. *Deinonychus*, with what seem to be the longest (relatively) forelimbs among presently known theropods, is characterized by the most prominent coracoid tubercle.

It is especially interesting that this correlation extends even to *Archaeopteryx*, a structurally similar, obligate biped. The theropod-like forelimbs (and pectoral arch) of *Archaeopteryx* are relatively longer than those of any known theropod, and correspondingly, the biceps tubercle is the most prominent of all. Furthermore, this tubercle in *Archaeopteryx* is situated at almost exactly the same position as in *Deinonychus*—just anterior to the glenoid rim and immediately ventral to the supracoracoid foramen. In my opinion, there can be little doubt that these are homologous structures, but for a more thorough treatment of the evolutionary relationships between *Archaeopteryx* and theropods see Ostrom 1973, 1974.

Inasmuch as the sternum is rarely preserved in theropod specimens, we do not know the exact position and orientation of the scapulocoracoid. Most articulated skeletons, however, indicate that the scapular blade ascended up and backward at an angle of between 20 and 40° to the axis of the dorsal vertebrae. For example, see the skeletons of *Struthiomimus altus*, AMNH
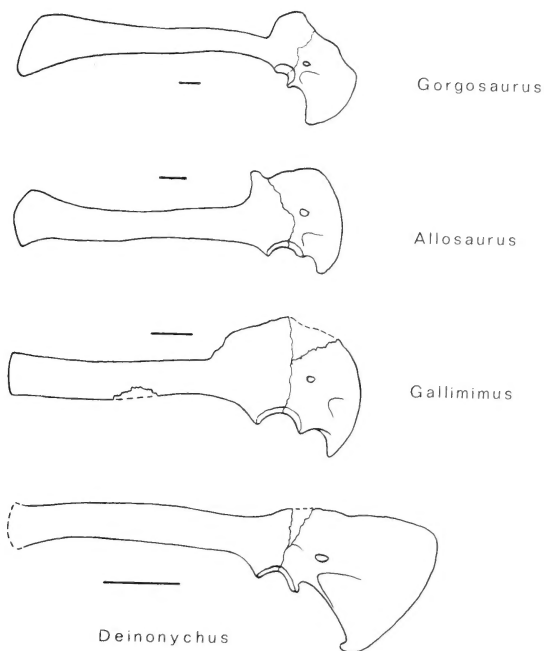
FIG. 2. Comparison of representative theropod scapulocoracoids to illustrate the relatively large size of the coracoid of *Deinonychus*. All scapulae are oriented horizontally and drawn to unit length for convenient comparison. The horizontal lines indicate respective scales; each line equals 5 cm. Taxa included represent the major theropod categories; Deinodontidae (*Gorgosaurus*), Megalosauridae (*Allosaurus*), Ornithomimidae (*Gallimimus*) and Dromaeosauridae (*Deinonychus*). All scapulae and coracoids are illustrated in a single plane; the anteromedial curvature of the coracoids is eliminated for uniform comparison.

5339 (pl. XXIV; Osborn, 1917); *Compsognathus longipes*, BS ASI563 (pl. III; Wagner, 1861); *Coelophysis longicollis*, AMNH 7223 (pl. 28; Colbert, 1961);

Velocirapter mongoliensis, GIMAS (pl. II, 2; Kielan-Jaworowska and Barsbold, 1972). In that position, the coracoid of *Deinonychus* would have been situated entirely anterior (and slightly medial) to the glenoid, with the supracoracoid foramen immediately in front of the glenoid and the coracoid tuber in front and slightly below that socket.

The reasons for the shape and unusual size of the coracoid in *Deinonychus* can only be guessed at, but there can be little doubt that they were related to forelimb function and the biomechanics of the shoulder joint. Reconstruction of the coracoid musculature provides some clues.

CORACOID MUSCULATURE

It is difficult to know which modern species is the best model for reconstruction of the pectoral and forelimb musculature in a theropod. Since *Deinonychus* is classified as reptilian, one is tempted to rely on a generalized modern reptile, such as *Sphenodon* or a lizard. But as obligate quadrupeds, in which the forelimb orientation and function as well as the scapulocoracoid position and morphology are very different, such analogues are of doubtful value. On the other hand, the scapula and humerus of *Deinonychus* (and those of many other theropods) are distinctly bird-like, even though the coracoid is not. Flight specializations seemingly disqualify all birds as suitable models, but birds—like theropods—are obligate bipeds. Hence the modern bird analogue may not be as inappropriate as it first appears.

If we accept the traditional conclusion that *Archaeopteryx* was a true bird (whether or not we accept it as the direct ancestor of modern birds), then we may assume that the pectoral anatomy of modern carinates evolved from a stage comparable to that of *Archaeopteryx*. Elsewhere (Ostrom, 1973; 1974; MSS), I have shown that the osteology of *Archaeopteryx* is fundamentally that of a small theropod. This is especially true of the forelimb and pectoral arch, including the coracoid! The coracoid of *Deinonychus*, for example, is far more similar to that of *Archaeopteryx* than it is to the coracoid of any living reptile. Parallelism and convergence notwithstanding, these pronounced skeletal similarities suggest (but do not establish) that the pectoral muscular patterns of *Archaeopteryx* and some theropods were also broadly similar.

In both living reptiles (*Sphenodon*, lizards and crocodilians) and birds the number of muscles that arise from the coracoid is few. The most important of those muscles are the M. coracobrachialis (often bipartite), M. supracoracoideus, M. subcoracoideus, M. biceps and M. sternocoracoideus. There are others, but these are the major muscles. With the exception of the sternocoracoideus, all insert on the forelimb and all but the biceps insert on the humerus. (In birds, the biceps has a second origin on the proximal medial crest of the humerus.) The principal function of the coracoid musculature is

to move the forelimb. Thus, the location of each muscle origin relative to the glenoid is of primary importance.

The significance of this last point is dramatically illustrated by discarding (for the moment) the conventional orientation (living position) of the scapulocoracoid and adopting instead a standard orientation of the glenoid, as in Figure 3. In that figure, all scapulocoracoids are oriented with the glenoid long-axis in a horizontal position. Despite the great morphological differences among the four species figured, there is surprising uniformity as regards the location of coracoid muscle origins with respect to the glenoid. In all four model species, the M. coracobrachialis pulls the humerus toward the coracoid (as we would expect). In a lizard (also *Sphenodon* and crocodilians) that movement is downward and slightly backward. In birds, however, it may be forward and slightly upward, or down and backward depending upon which portion of the coracobrachialis is contracting. In all four groups, the biceps is a primary fore-arm flexor, and the coracoid origin of such flexors obviously must lie on the "flexion" side of the glenoid (i.e., the origin must be situated between the glenoid and the insertion point on the adducting antebrachium). The close correspondence of the origin areas of the coracobrachialis (and supracoracoideus) and the biceps, as shown in Figure 3, assures that the plane of fore-arm flexion (by the biceps) coincides with the planes of humeral adduction produced by these other coracoid muscles. Thus, fore-arm flexion in a lizard adducts the distal limb segments ventromedially, whereas the avian fore-arm is flexed anteromedially.

From these living models, it is evident that the main function of those muscles that originate on the coracoid is adduction of the humerus and adductive flexion of the fore-arm at the elbow. The direction of humeral adduction and fore-arm flexion is determined by the orientation of the scapulocoracoid and the location of the muscular origins with respect to the glenoid. These observations are so elementary that they hardly need mention here.

However, regardless of what particular anatomical terms happen to be applied to the muscles that arose from the theropod coracoid, and regardless of whether they are considered homologous with those of modern reptiles or birds, it is certain that the same actions and movements must have occurred. Accepting the scapulocoracoid orientation that is indicated by the several theropod specimens cited above, the coracoid musculature of *Deinonychus* must have produced powerful anteromedial adduction of the humerus, coupled with strong anteromedial flexion of the fore-arms and hands. Humeral adduction presumably was accomplished by relatively large "coracobrachialis" and "supracoracoideus" muscles that originated on the large anterior expansion of the coracoid. Anteromedial flexion of the antebrachium was accomplished by a powerful "biceps" that probably arose by tendonous attachment on the prominent coracoid tuber (biceps tubercle). This latter feature is ideally situated for that function, anterior and medial to the glenoid, and corresponds closely in position and form to the biceps tubercle of *Archaeopteryx* (Walker, 1972).
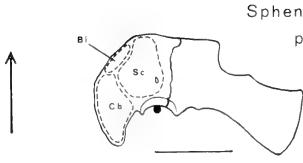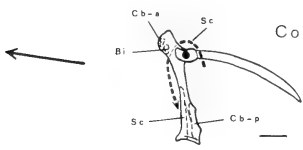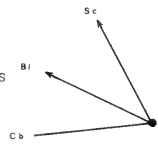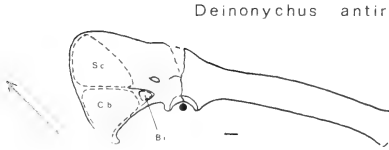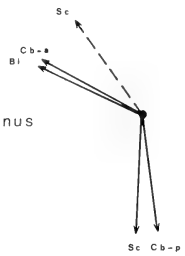
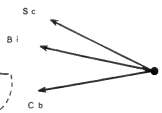Sphenodon punctatum
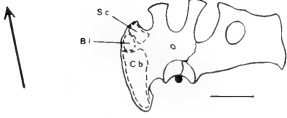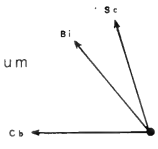
Iguana iguana
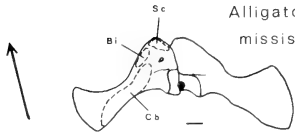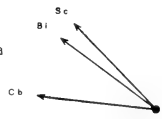
Alligator mississippiensis

Corvus americanus

Deinonychus antirrhopus

APPENDICULAR EVIDENCE

The humerus of *Deinonychus* has been described previously (Ostrom, 1969b) and does not require detailed description here. Some review is appropriate, however, as regards the preceding interpretation of the coracoid and its musculature.

As noted in the above report, good evidence exists (the large deltopectoral crest) in the known humeri of *Deinonychus* that indicates powerful forward adduction of the forelimbs by large pectoralis and coracobrachialis muscles. The opposite, recovery movement by the M. deltoideus apparently was not so powerful, judging from the low profile (Fig. 1) of the incomplete acromial process of the scapula. While the large deltopectoral crest does indicate a large pectoralis muscle with considerable leverage, there are no distinct scars preserved on that structure or on adjacent surfaces to show the relative sizes of the pectoralis vs. the coracobrachialis. It is presumed, however, on the basis of the coracobrachialis insertion site in both modern birds and reptiles, that this muscle inserted proximally along the base of the deltopectoral crest on the medial (ventral) humeral surface adjacent to the insertion of the M. pectoralis. Its action, like that of the pectoralis, was anteromedial adduction of the humerus.

A small but distinct tubercle (marked by the uppermost line labeled "PE"

FIG. 3, opposite page. The scapulocoracoids (in lateral view) of three modern reptiles and a bird (common crow) showing the attachment areas of three major muscles that originate on the coracoid. Since these muscles function exclusively to move the humerus or flex the antebrachium, their positions relative to the glenoid are the critical mechanical features. For that reason, the scapulocoracoids are illustrated here with the glenoids oriented in standard position (i.e., the long axis of each glenoid is horizontal, regardless of its natural position in life). The living position of each example is indicated by the arrow at the left, which points anteriorly and indicates the horizontal. At the bottom is the scapulocoracoid of *Deinonychus* showing the probable areas of origin proposed here for the coracoid musculature. The clusters of arrows at the right indicate the direction from the glenoid (indicated by the solid spot) to the center of origin of the several coracoid muscles (usually, but not always the same as the direction of muscle pull). In the quadrupedal examples, the coracoid muscle-origin locations are basically similar. In birds, the locations of muscle origins are different, but the directions of muscle pull are surprisingly similar to that of the quadrupedal examples. The supracoracoideus (of birds) pulls the humerus up and forward (dashed arrow), by virtue of its passage upward from the humerus through the foramen triosseum and then downward to its origin on the ventral extremity of the coracoid. The coracobrachialis anterior, with its origin adjacent to that of the biceps on the enlarged avian biceps tubercle, functions like the coracobrachialis (unmodified) of the quadrupeds (i.e., adducting the humerus in nearly the same plane as antebrachial flexion by the biceps), whereas the coracobrachialis posterior appears to be a remnant of the primitive muscle that retained the primitive origin site adjacent to the sternal border of the coracoid. The latter now functions to adduct the humerus posteroventrally (folding the wing). Abbreviations: *Bi* = M. biceps; *Cb* = M. coracobrachialis; *Cb-a* = M. coracobrachialis anterior; *Cb-p* = M. coracobrachialis posterior; *Sc* = M. supracoracoideus. The horizontal lines beneath each scapulocoracoid equal 1.0 cm, all coracoids being drawn to unit length for easy comparison.

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