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GENERAL NOTES

The humeroulnar pulley and its evolution in hummingbirds.—The humeroulnar pulley or trochlea humeroulnaris (*in* Nomina Anatomica Avium, J. J. Baumel et al., eds., Academic Press, London, England, 1979) is a ligament of the elbow in most birds (Fig. 1d). Originally named by Shufeldt (Myology of the Raven, McMillan and Co., London, England, 1890), the ligament extends from the caudal aspect of the medial epicondyle of the humerus to the ventral surface of the proximal end of the ulna. Buri (Jenaische Z. Naturwiss. 33:361–610, 1900) referred to the pulley (his "Ringband" and "Sehenschlinge") and noted some differences among different families. Sy (J. für Ornith. 84:199–296, 1936) illustrated the pulley but did not discuss its relation to M. flexor carpi ulnaris (FCU). More recently, the pulley has been mentioned in connection with its relationship to M. expansor secundariorum (Berger, J. Morph. 99:137–168, 1956), as well as in descriptive myology (Berger, Auk 85:594–616, 1968; Raikow, Auk 94:331–342, 1977). In none of these works has the pulley been thoroughly described and compared. The implication has been that, with few exceptions, this structure is essentially uniform. The purposes of this paper are to describe the structure and function of the pulley in its generalized state, to draw attention to its diversity, and to explain the unique pulley of hummingbirds (Trochilidae).

Our interest in the humeroulnar pulley grew out of our recent investigation of hummingbird myology. The pulley in hummingbirds is so unusual that we were compelled to look elsewhere to determine its homologies with a "normal" pulley. After dissecting representative forms from over 40 families, we determined the apparent ancestral condition for modern birds (Fig. 1b). Directional terms (dorsal, ventral and caudal) refer to the horizontally extended wing.

In most birds the pulley is best seen in ventral view. Its main structure can be likened to a loop, the cut ends of which have been spread sideways and attached to different bones (Fig. 1c). Ancestrally, it consists of three main parts that we call A, B and C (Fig. 1b). The main origin of the pulley, A or pars humeralis, is from the humerus. It arises from the caudolateral surface of the medial epicondyle of the humerus and passes superficial to the proximal portion of the tendon of M. flexor carpi ulnaris. It continues around and deep to that tendon (our part B or pars ulnaris) and inserts on the ventral surface of the ulna between the olecranon and the insertion of ligamentum collaterale ventrale. There is no demarcation between A and B in some birds; in others they are separated by an ossified or cartilaginous swelling of the pulley. A second humeral component, C or pars humeralis accessoria, arises from the ventral surface of the medial epicondyle of the humerus ventral and slightly distal to the origin of ligamentum collaterale ventrale. This component passes distally to join the main portion of the pulley between A and B. Pars humeralis (A) may be fused or unfused to the proximal end of the tendon of FCU. Pars humeralis accessoria (C) varies not only in size but in its proximity to A. Pars ulnaris (B) is the most constant feature, being present in all forms that have a pulley. We do not recommend use of the terms pars tendinea and pars pennata as introduced and described for the Rock Dove (*Columba livia*) in J. J. Baumel et al. (1979:152) because we regard pars tendinea as a synonym of trochlea humeroulnaris, and pars pennata to be a largely tendinous portion of M. expansor secundariorum.

The primary function of the pulley is to keep the belly of FCU in constant relation to the ulna. That is, in extreme flexion of the forearm the pulley prohibits the tendon and belly of FCU from moving proximally along the humerus. It (especially C) also helps to bind the elbow against separation at its medial surface. The pulley may also function as a point of origin for one of three parts of M. expansor secundariorum (ES). Humeral and scapular origins of ES are not considered here and all further references to that muscle refer to the

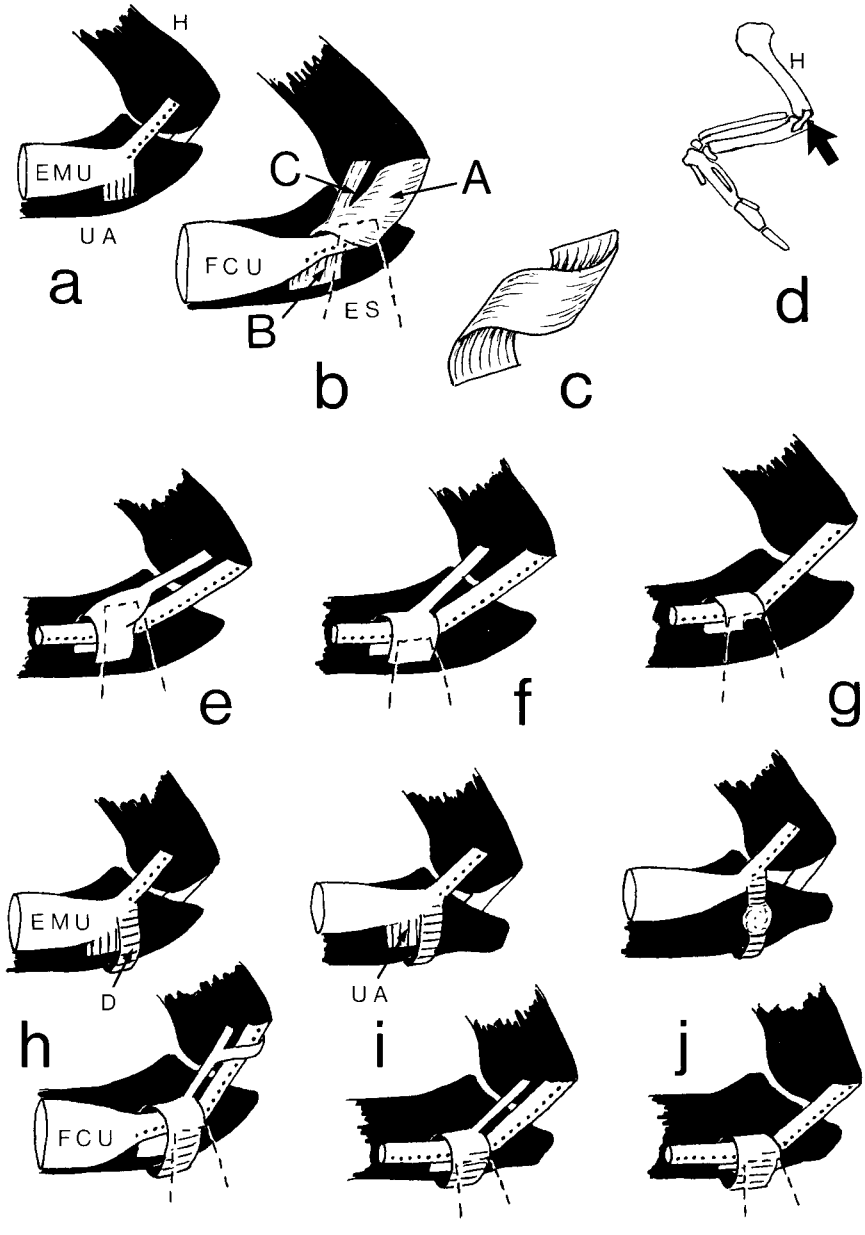

FIG. 1. Diagrams of the humeroulnar pulley and its associated structures: a. dorsal view of elbow. b. ventral view of elbow showing generalized form of pulley: A = pars humeralis; B = pars ulnaris; C = pars humeralis accessoria. c. diagram of parts A and B to show main structure of pulley. d. right wing, ventral view, showing location of pulley. e, f, g. ventral

portion from the humeroulnar pulley (Fig. 1b). In a few orders ES contributes to the stabilization of FCU, but primitively it arises directly from the pulley and has no relation to that muscle.

An essentially primitive form of the pulley is characteristic of the Sulidae, Ardeidae, Anatidae, Rallidae, Charadriidae, Falconiformes, Galliformes, and the majority of land birds from pigeons (Columbidae) to the passerines (Passeriformes). The typical oscine pulley is very reminiscent of the ancestral form described above with one important exception. The tendinous origin of ES from the pulley has shifted somewhat caudally and distally and, in combination with B, has acquired the additional function of guiding the tendon of FCU. The need for A is correspondingly reduced, and A is weak in some passerines. Reduction or loss of C may also occur. Loss of one or both of the humeral components of the pulley (A and C) appears to have occurred independently in unrelated groups. In most suboscines A is reduced to a slender band that crosses the tendon of FCU and C is present but noticeably reduced (Fig. 1h). In the swifts (Apodidae) only C is present (Fig. 1i), and in the crested-swifts A is present, but C is lost. In the Tinamidae only B is present (Fig. 1g). It serves as a point of origin for ES which, together with B, forms a hook that restrains the tendon of FCU. Columbidae lack C and ES is ligamentous. In the Procellariidae (Fig. 1f) and Laridae (Fig. 1e) B forms a loop on the ulna and C is present; ES plays no role in restraining the tendon of FCU. In at least one family (Spheniscidae), FCU is represented only by a tendon and the pulley is absent.

In hummingbirds both A and C are lost (Fig. 1j); only the attachment to the ulna (B) remains. In addition, a ligamentous sling (D) containing a large sesamoid arises from the tendon of origin of M. extensor metacarpi ulnaris, passes around the caudal border of the ulna, and fuses with what remains of the pulley. The tendon of FCU passes through the loop formed by this sling and the pulley (B). ES arises from the pulley and also serves to guide the tendon of FCU. Other differences between the ancestral condition and that of hummingbirds become more meaningful when the ulnar anchor is understood and morphological intermediates are examined (Fig. 1h, i, j).

The ulnar anchor, a short tendinous slip, arises from the tendon of origin of M. extensor metacarpi ulnaris, a large muscle on the dorsal side of the forearm in most birds. The anchor passes caudally and inserts on the caudodorsal surface of the ulna (Fig. 1a, h, i). Investigation of the myology of hummingbirds alone might lead one to conclude that the ligamentous sling (D) represents a modified ulnar anchor. However, in suboscines and swifts, both a ligamentous sling and an ulnar anchor are present (Fig. 1h, i). Hummingbirds lack the ulnar anchor. Thus, the humeroulnar pulley of hummingbirds probably evolved from the primitive condition by loss of A and C and the ulnar anchor, and elaboration of a new structure, D, found elsewhere only in swifts and suboscines.

This paper represents a cursory survey of variation in the humeroulnar pulley, based on only a single species from most of the families examined. In view of its structural diversity we recommend that a detailed description of the humeroulnar pulley be included in future works on the wing muscles of birds.—GREGORY DEAN BENTZ AND RICHARD L. ZUSI, *National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.* (Present address GDB: *Mount Vernon College, Washington, D.C. 20007.*) *Accepted 1 Dec. 1980.*

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views showing pulleys of Laridae, Procellariidae and Tinamidae, respectively. h, i, j. dorsal views (above) and ventral views (below) of a suboscine, Apodidae and Trochilidae, respectively. D = tendinous sling; EMU = M. extensor metacarpi ulnaris; ES = M. expansor secundariorum; FCU = M. flexor carpi ulnaris; H = humerus. Bones are black; muscle tendons shaded with dots; ulnar anchor vertically hatched; tendinous sling (D) horizontally hatched; M. expansor secundariorum shown as if transparent by dashed outline.