AVIAN ANATOMY AND THE ANATOMIST

By M. JOLLIE

Berger (1956*a*) summarized the anatomical variations found in man in four areas of study, namely neurology, myology, osteology, and angiology, with the purpose of demonstrating the kinds of variation to be expected and evaluated in birds. I would like to discuss the obvious, additional category, variations attributable to the anatomist and not to the anatomy of the subject.

An example of an area of disagreement in interpretation is supplied by the description of the muscle known as the "expansor secundariorum" of the pigeon presented by Berger (1956*b*). The "expansor secundariorum" is an extremely difficult structure to study, lying as it does embedded in the subcutaneous connective tissue and associated in part with the strong bracing connective tissue behind and within the axilla of the wing. I am of the opinion that most anatomists have preferred not to describe this area; therefore, it is with considerable hesitation that I attempt to alter the present concepts.

I can agree with Berger that sometimes there are two structures involved in this complex. Occasionally there is a minute muscle belly which, as in the pigeon, *Columba livia* (fig. 1), arises off the connective tissue band from the axilla and inserts in common with the triceps. This muscle is properly, as suggested, a part of the triceps; it can be identified as the pars axillaris. The main "muscle" is a part of a complex or series which is not clearly understandable in terms of Berger's description, in which it is assumed that the muscle fibers associated with the axillary tendon form the belly of a skeletal muscle.

Before discussing the muscle let us consider its "tendon," which may be but one band within the connective tissue of this area. This connective tissue has the function of holding the skin tightly to the base of the wing. Fibers extend out to the skin from the region of insertion of the latissimus dorsi and also from behind the shoulder joint and from the strong connective tissue enclosing the axillary nerves and blood vessels. Within the axillary mass, and sometimes dorsally, small bands frequently can be detected and occasionally these are continuous with the "tendon" described for the "expansor secundariorum." Even when such a "tendon" is lacking, a "vestigial" attachment may be observed in the axilla. Dorsally there may be a strong connective tissue brace for the humeral (better called scapular) tract of feathers.

The relationship between the muscle fibers of the "expansor secundariorum" and the band of connective tissue from the axilla is a direct one, since this band is a functional response to the need for anchorage of a part of this muscle complex (therefore not really in disagreement with Fürbringer, 1902:575). This band may be used in the origin of other parts; it may be an important area of origin. The configuration of the base of the wing apparently determines whether an axillary connective-tissue band is needed.

Because of its erratic functional nature and because it is not associated primarily with a skeletal muscle, this band is not properly a tendon. It might best be called a secondary tendon or brace. In the case of the passerines (fig. 2) the axillary accessory is replaced by a marginal one. The explanation may be that the dorsal brace to the scapular (humeral) tract functionally replaces the more ventral one. The axillary "tendon" is not a vestige of a once better developed muscle; it is a specialization in those species where it occurs.

The muscle fibers in question are modified from those associated with the feathers; these are typically diagonally disposed. The "expansor secundariorum" is made up of a well-developed group of such feather muscles which serves two purposes: (1) depres-

sion of the secondaries and tertiaries (that is, it resists their upward displacement in flight) and (2) drawing them medially so as to increase the support area of the inner wing. The depressors of the secondaries arise off the thickened fascia of the posterior ventral margin of the wing; medially this is anchored to the distal end of the humerus (or the humeroulnar ligament) and braced in the pigeon by the tendon-like band from the axilla. The depressors become weaker as one proceeds distally along the ulna four or five secondaries. There is a smaller series of antagonistic dorsal muscles for the secondaries and their coverts.

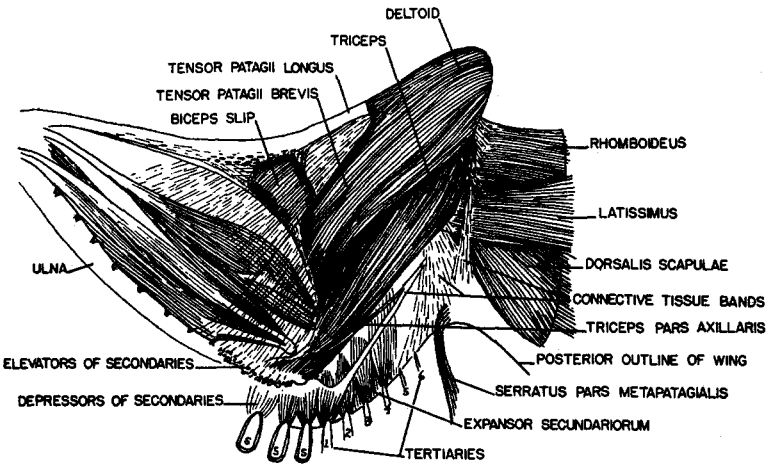

Fig. 1. Dorsal view of dissected wing of the pigeon, *Columba livia*

The description (and figures) of the expansor secundariorum of the Crow (*Corvus brachyrhynchos*) by Hudson and Lanzillotti (1955) does not apply to the Raven (*Corvus corax*). In this latter species (fig. 2) there is no axillary band but there is one which extends from the fibers of the depressor-adductors of the tertiaries to the posterior end of the scapular (humeral) tract of feathers (at the insertion of the pars metapatagialis of the serratus muscle). This same area is braced by connective tissue extending back from the axilla and from the shoulder area in general.

The marginal connective tissue band of the metapatagium lies below the quills of the tertiaries and is continuous with their sheaths. Midway toward the elbow, muscle fibers arise off the skin and from this band; these insert in part on the connective tissue sheaths of the inner tertiary quills. Many of the fibers parallel the line of the band and continue to the area just before the elbow where they insert on the quills of the outer tertiaries and the inner secondaries. Hudson and Lanzillotti (*op. cit.*:23) have described the remainder of this series, that is, the depressor fibers of the secondaries. The dorsal elevators of the secondaries are very weakly developed in the Raven.

Berger (1956*b*:153) has pointed out that the "expansor secundariorum" is composed of smooth muscle fibers while those of the humeral or forearm origin, which depress the secondaries, are striated. Whether a muscle is smooth or striated is dependent in part on its function. The assumption that the depressors of the secondaries are part of the "M. flexor carpi ulnaris" will have to be demonstrated although this is a possibility.

Another example of difference in interpretation is supplied by description of the pec-

toralis as double or single, that is, the pectoralis of the Whooping Crane (*Grus americana*) is described by Fisher and Goodman (1955:45), as having a superficial and a deep layer, whereas I would prefer to describe it as a unit. Garrod (1876:340) listed species in which he believed the muscle was double while Gadow and Selenka (1891:243) pointed out that the tendency to have semi-separate layers is more marked in young birds.

Fisher encountered the two-parted condition of the pectoralis in the cathartid vultures (1946) and assumed (in conversation) that this represented an adaptation for soaring. He was much surprised at my report that this muscle did not have two parts in the eagles *Aquila chrysaëtos* and *Uroaëtus audax* although there was individual variation ranging from slight separation to distinct but incomplete separation. Fürbringer

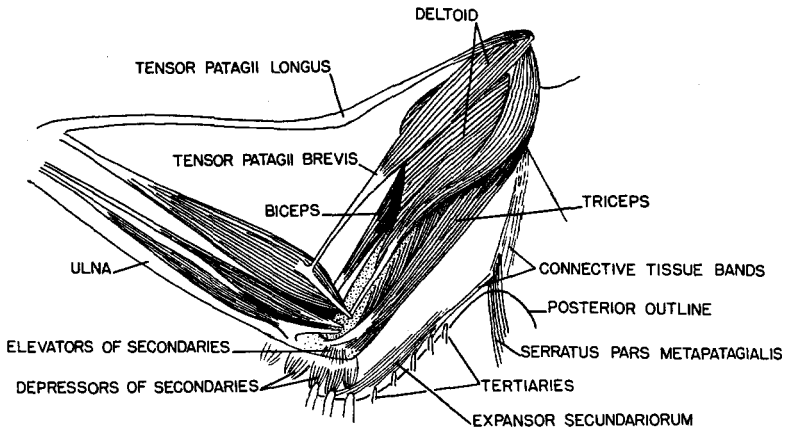

Fig. 2. Dorsal view of dissected wing of the Raven, *Corvus corax*; muscles overlying the scapula not shown.

(1888:422) reported the muscle of *Uroaëtus* and *Torgos* as double; my dissections of these genera do not support this conclusion. The problem here is to decide when this muscle is double. In my opinion it should be described as two parted only when there is total separation as in the cathartids or *Fregata*. To imply that it is double when in fact it is only partly so results in confusion.

A last example can be drawn from figure 33 in Hudson and Lanzillotti (1955) which shows the patagial fan of the Prairie Falcon (*Falco mexicanus*). In my dissections of the genus *Falco* and related genera I have never observed this style of fan. The difference is most likely due to the dissector. This same observation applies to some of the illustrations in Fürbringer (1888). The problem here is much like that of the metapatagium; in the separation of tendinous bands from the sheets of fascia, one really does not know where the one begins and the other leaves off; it is a matter of interpretation just how the fan should look. For a comparative study, it is necessary that all of the dissections be made by a single person. Otherwise the range of variation is greatly increased. Contrasting human and avian anatomy in this respect, it should be pointed out that the former is so well known that details can profitably be described; in the latter the general picture is still rather hazy.

In summary, I would stress the fact that certain aspects of avian anatomy are difficult to study and to interpret. What may be recorded in the literature as individual variation or specific variation may only be a matter of interpretation. This type of variation necessitates continual testing through parallel dissection until such time as our

knowledge is sufficient that we recognize significant and real differences when we encounter them.

The research for this commentary was a part of that directed toward the problem of the anatomy and phylogeny of the diurnal birds of prey. This project was supported by a National Science Foundation Grant (NSF G–1737).

LITERATURE CITED

Berger, A. J.

1956*a*. Anatomical variation and avian anatomy. Condor, 58:433–441.

1956*b*. The expansor secundariorum muscle, with special reference to passerine birds. Jour. Morph., 99:137–167.

Fisher, H. I.

1946. Adaptations and comparative anatomy of the locomotor apparatus of new world vultures. Amer. Midl. Nat., 35:545–727.

Fisher, H. I., and Goodman, D. C.

1955. The myology of the whooping crane, *Grus americana*. Illinois Biol. Monog., 24:viii+127 pp.

Fürbringer, M.

1888. Untersuchungen zur Morphologie und Systematik der Vögel zugleich en Beitrag zur anatomie der Stütz- und Bewegungsorgane (T. J. van Holkema, Amsterdam) 2 vols., xlix+1751.

1902. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jena. Zeitschr. für Naturwiss., 36:289–736.

Gadow, H., and Selenka, E.

1891. Vögel: Aves. I. Anatomischer Theil. *In* Bronn's Klassen und Ordnungen des Thier-Reichs, vol. 6 (Abt. 4) (C. F. Wintersche, Leipzig and Heidelberg) iv+1008 pp.

Garrod, A. H.

1876. Notes on the anatomy of *Plotus anhinga*. Proc. Zool. Soc. London (1876):335–345.

Hudson, G. E., and Lanzillotti, P. J.

1955. Gross anatomy of the wing muscles in the family Corvidae. Amer. Midl. Nat., 53:1–44.

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania.