ANATOMICAL VARIATION AND AVIAN ANATOMY

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Fisher (1955:69) called attention to the urgent need for more information on the amount of morphological variability "in a homogeneous series within a species." Fisher and Goodman (1955:119), in a thorough investigation of the myology of the Whooping Crane (*Grus americana*), were impressed by "the great variability that may exist in the conformation of muscles and, apparently, in the pathways of nerves to the muscles," and by the fact that "the extent of variation [in the brachial plexus] between individuals is of no greater scope than that . . . between the sides of an individual."

It seems desirable, therefore, to examine anatomical variation in general, with special reference to its bearing on the phylogeny of birds. Under four headings—neurology, myology, osteology, and angiology—I propose to point out certain basic concepts or principles derived from the accumulated morphological knowledge of the best-known mammal, man, and to include information on variation in birds.

Morphological variation is, of course, the rule, not the exception. This is one of the first things to be learned by the beginning student of human anatomy. Although there is a basic typical design for each vertebrate class, or order, or family, no two animals, however closely related, have exactly the same conformation in the minute structure of all organ systems. One cannot by knowing the pattern on one side of a body predict the pattern on the opposite side, although one might predict that they would be the same in a certain percentage of cases. In order to make such a prediction, however, one needs a mass of data obtained from hundreds of dissections, which enable one to visualize clearly the normal limits of variation. Consequently, it should be emphasized at the start that the particular pattern on one side of a body need exhibit no more similarity to the pattern on the opposite side than to the pattern in some other body. Ornithologists should not be surprised, therefore, when it is pointed out that the pattern of the brachial plexus or the vascular system differs in the two wings or two legs of one specimen.

NEUROLOGY

For the present purpose, we need discuss only the brachial plexus and some of its terminal branches. A plexus is a "network or tangle, chiefly of veins or nerves" (Dorland, 1945:1146). Specifically, the brachial plexus is a network by which the nerve components associated with certain spinal nerves are rearranged. It has a general, but not invariable, pattern characteristic for each group of animals. In man the brachial plexus is typically formed from the anterior primary rami of the last four cervical spinal nerves (nos. 5–8) and the first thoracic spinal nerve, but in many cases (62 per cent of 175 plexuses in one study) the plexus receives contributions from the fourth cervical nerve; it often receives small twigs from the second thoracic nerve as well. Furthermore, the entire plexus may be shifted a segment cephalad or caudad, in which event the plexus is said to be prefixed or postfixed, respectively (see Kerr, 1918). There is also considerable variation in the gross pattern of this plexus when it is formed from the usual spinal nerves.

Now with respect to the terminal branches of the brachial plexus, M. teres major, in man, is innervated by the lower subscapular nerve. This nerve typically is a separate branch of the posterior cord of the brachial plexus, but not infrequently it arises by a common trunk either with the thoracodorsal nerve or the axillary nerve. Again, the musculocutaneous nerve, arising from the lateral cord of the plexus, innervates the preaxial muscles of the arm and then terminates as a cutaneous nerve. This nerve typically pierces M. coracobrachialis, innervates it, and then passes distad in the interval

between Mm. biceps brachii and brachialis, sending branches to them. But the musculo-cutaneous nerve does not always pierce the coracobrachialis muscle. That muscle may receive a branch(es) from the nerve, or a separate, more proximal, branch directly from the lateral cord. In the latter case, the definitive musculocutaneous nerve simply passes along the coracobrachialis muscle without sending branches to it. In some bodies, the musculocutaneous nerve sends, at a variable level, a ramus to join the median nerve, a nerve which innervates no muscles in the arm and gives off no branches there. The median nerve itself is formed by the union of rami derived from the medial and lateral cords of the brachial plexus, but the site of union may be located at any level from the axilla almost to the elbow.

All of these and other differences from the "typical" pattern are considered to fall within the normal limits of variation. They are not pathological, and they do not inter-fere with the functioning of the muscles innervated. Considering these differences to represent normal variation, how can one interpret or explain such variation from a genetically established plan? Up to a point, the explanation is relatively simple. What is spoken of grossly as a "nerve" is actually a structure composed of hundreds of nerve fibers arranged in bundles or funiculi held together and surrounded by connective tissue. The nerve cell bodies of the neurons whose axons form the motor components of the median nerve are located in the ventral horn gray of the sixth, seventh, and eighth (some-times also the fifth) cervical and the first thoracic segments of the spinal cord. Assum-ing, within limits, nerve-muscle specificity between nerve-cell columns in the spinal cord and certain muscle groups, it matters little what course or path the axons follow to reach those muscles. All that is necessary is that the axons do reach them—this is one of the key problems in effecting a successful re-innervation of a muscle after its motor supply has been cut. Thus, the ramus of the musculocutaneous nerve which joins the median nerve in the lower arm contains axons derived from the median nerve portion of the motor cell column in the spinal cord. Those neurons are not destined to innervate pre-axial muscles of the arm and, therefore, sooner or later, they rejoin the median nerve in order to reach their proper termination. It seems reasonable to expect similar varia-tions in the gross pattern of the definitive nerves from the bird brachial plexus. We should, indeed, be surprised if such variation were not found.

Even though we may assume that the gross pattern of the brachial plexus has a genetic basis, such variations as those discussed above do not cast doubt on the phylo-genetic relationships of individuals of *Homo sapiens*. One should not, therefore, place undue emphasis on such variation in birds. The gross pattern of the brachial plexus *per se* reveals very little about the ultimate innervation of the muscles. Not until local-ization of the cell columns in the spinal cords has been determined (by means of neuron chromatolysis experiments), will much really be known about the innervation of the appendicular muscles of birds. Furthermore, it is scientifically naive to assume that the gross nerve supply of a muscle is the same in all genera or families of birds. Hence, it would be uncritical when discussing the myology, but not the neurology, of cuckoos, for example, to cite from Fisher (1946) the innervation of the muscles as he found it in the vultures. What justification is there for quoting from the few workers (Fürbringer, Gadow, Howell, Fisher) who have studied the innervation of avian muscles? Such refer-ence has meaning when one compares published data with original data on the same or another group of birds, or when one presents a compilation which attempts to summarize nerve-muscle relationships in birds. Even then, the limitations inherent in dealing only with gross patterns must be recognized.

Nevertheless, we do need to know much more about the gross relationships between muscles and nerves in birds. There is, relatively, so little known about the total appen-

dicular myology of birds, however, that the new student of avian anatomy should not be distracted by a pedantic concern with the homology of muscles outside the class Aves.

<div align="center">MYOLOGY</div>

In general, the muscular system is more stable than the nervous or vascular systems. One frequently encounters difficulties in attempting to generalize, but it might be said that, in man, more variation is to be expected in the distal muscles of the extremities, or in muscles having an extensive origin, such as M. pectoralis major, than in more proximally located muscles or those having a small, discrete origin, such as the long head of M. biceps brachii. There are, of course, exceptions to such a broad statement. The fact is, however, that variations in the configuration of muscles are relatively frequent, but mostly minor in nature. Small accessory heads, bellies, or tendons of the forearm muscles are common in man, but their presence does not complicate the interpretation of the musculature of that region. In rare instances, a muscle such as the coracobrachialis or biceps brachii may be absent. Such variations from the usual pattern are spoken of as anomalies. One would not in view of even the complete absence of a muscle contemplate assigning the individual to a different species or genus. In man, the anomaly can be recognized as such because the total myology of the human body is so well known.

We do not know that much about avian anatomy. We know, in fact, very little about intraspecific variation in the myology of birds. Therein lies the great need for many detailed studies of avian myology. Careful dissections, with accompanying detailed descriptions and measurements, of all of the appendicular muscles in 200 or 300 individuals of a given species would undoubtedly reveal many interesting facts. Until such data are available, the anatomist has no choice but to record details and interpret them in the light of his experience. The most interesting and significant taxonomic problems in avian anatomy frequently involve "aberrant" genera of which one is fortunate to obtain even two adequately preserved alcoholic specimens. Moreover, if one attempts a critical analysis of the muscles of any given group of birds, one soon discovers that all too little is known about the configuration and relative development of individual muscles in the various families and orders of birds. I decided several years ago that I could not interpret adequately data on the myology of the Cuculidae until I knew more about the nature of certain muscles and muscle-groups in other orders.

The following are examples of variation in bird muscles. Fisher and Goodman (1955:120) found that "in three of our six dissections of the Whooping Crane, M. pectoralis utilized the well developed tracheal enclosure for part of its origin." They noted also that M. latissimus dorsi metapatagialis is variable in development and may be absent and that the belly of M. flexor perforans et perforatus digiti II may or may not be bipennate. Hudson and Lanzillotti (1955:39) found M. flexor pollicis in only two crow wings "out of 22 wings of the crow and six of the raven," and (pp. 34–35) they found a unilateral variation of M. extensor indicis longus in *Cyanocorax*: "on the left side the origin is from the radius only, as usual, but on the right side there is a distinct extra head of origin from the ulna. In one specimen of *Aphelocoma coerulescens californica* both sides have an ulnar attachment." Fürbringer (1902:536) noted the absence of M. deltoideus minor, perhaps as an individual variation, in *Cypselus*. Beddard (1898: 309) stated that M. latissimus dorsi, pars posterior, is sometimes absent in pigeons and that, according to Fürbringer, "its occasional absence is a matter of individual variation."

More is known about individual variation in the ambiens muscle, probably because it is one of the "formulae" muscles and, therefore, has been studied more intensively. This muscle is present in some genera of parrots, absent in others. "*Stringops* is peculiar in that the muscle is sometimes complete and quite normally developed, and sometimes

ends in a thin tendon on the capsule of the knee joint. This recalls *Oedicnemus*" (Beddard, 1898:261). Similar variations have been reported in *Opisthocomus*, *Phaëthon* and some of the Procellariiformes (Beddard, 1898:289, 405, 448).

Fisher and Goodman (1955:85, 123) emphasized the amount of variation they found in M. caudofemoralis (piriformis) in three specimens of the Whooping Crane, and they discussed other differences in the muscle formulae of cranes found by the several investigators of that group. Their report is especially significant because the two parts of M. caudofemoralis are widely used in the muscle formulae of Garrod. Both parts (pars caudofemoralis and pars iliofemoralis) of this muscle were found in two specimens of the Whooping Crane, but only pars iliofemoralis in a third specimen. In one dissection, they found three parts to the muscle. I found both parts of this muscle in three specimens of the Sandhill Crane (*Grus canadensis tabida*).

A basic question is involved here. Several anatomists in recent years have emphasized the necessity for knowing the complete appendicular myology of birds and not just the leg-muscle formulae. These formulae are convenient items to tack on to the technical diagnoses of families and orders of birds and all standard references give credence to this amount of myological data. Beddard's (1898:367) brief report on variation in the muscle formulae in the Gruidae should have cast doubt on the validity of these muscles for solving taxonomic problems. Fisher and Goodman (1955:124) stated: "Thus it is impossible with the information at hand to set up any definite formula for the family Gruidae, or apparently even for the genera *Grus* and *Balearica* as now known. One would not expect intraspecific variation of the sort we noted or that found by Mitchell and Beddard in *Balearica* . . . . The variation of *G. leucogeranus* from the *Grus* line is not unexpected, for this crane also differs in many other ways." If, however, leg muscle formulae were as diagnostic as they were thought to be, these differences would not be found. As far as these muscles are concerned, it is possible that the cranes present one of the more troublesome groups. One would not, as Fisher and Goodman stated, expect this amount of intraspecific (or intrageneric) variation in a muscle complex unless it were in the process of "dropping-out" phylogenetically, in which case one might expect considerable variation. How much of this variation in the cranes falls under the heading of anomaly? One would surmise that the "normal" or "typical" pattern for the genus *Grus* is the presence of both parts of M. caudofemoralis. At the same time, certain features in the development of pars caudofemoralis suggest that it might be in the process of becoming vestigial in certain groups of birds. In a bird the size of the Sandhill Crane, for example, the belly of pars caudofemoralis is only 9 cm. long and has a maximum width of less than 1 cm.; the tendon of origin is but 0.5 mm. in diameter. Relative to its development in some other birds, pars caudofemoralis might be considered rudimentary in the cranes. The relatively small size of the muscle in some genera, however, may be only a reflection of locomotor habits.

The absence of a given muscle in a single specimen of a species or genus does not necessarily mean, however, that that muscle is not characteristic for the species or the genus or that the muscle is useless as a taxonomic character, either for that group or for other groups. After one dissects a number of closely related genera, one quickly recognizes deviations from the typical pattern. One must realize that one may be dealing with an anomaly, a situation which does not negate all of the other evidence.

One other point of variation in the cranes deserves mention. Gadow and Selenka (1891:142) and Hudson (1937:60, 69) reported that they did not find M. iliotrochantericus medius in the genus *Grus*, but Fisher and Goodman (1955:123) found it in *G. americana* and *G. canadensis*. I found this muscle bilaterally in two specimens and unilaterally in a third specimen of *G. canadensis tabida*. In each of my dissections, however,

there was evident fusion between Mm. iliotrochantericus medius and anterior; the two muscles were separate at their origins, but the bellies fused distally to insert by a common tendon. In the right hip of the one specimen, the two muscles were completely fused, so that this complex was represented by a single muscle mass, arising, however, from the same area as that occupied by both muscles in the other dissections. Such fusion is not rare phylogenetically when two muscles arise or insert on adjacent areas and when their fibers have a generally parallel course. One may also recall both the phylogenetic and the ontogenetic differentiation of separate muscles from primitive muscle masses.

Thus it is clear that much needs to be known not only about intraspecific variation of muscles, but also about the presence or absence and the relative development of the appendicular muscles throughout the families and orders of birds. Relative development is not indicated by a simple muscle formula. No region has received adequate attention throughout the orders of birds. The excellent series of papers on the head (Barnikol, 1952, 1953a, 1953b; Hofer, 1950; Starck and Barnikol, 1954) serves to emphasize the need for additional comparative studies.

<div align="center">OSTEOLOGY</div>

Less tedious than myology, the osteology of birds has received more attention. More adequate series of skeletons are available than of alcoholic specimens, although articulated skeletons are all too rare in many collections. The difficulties encountered in dealing with inadequate series of skeletons were well expressed by Lucas (1893:52): "Unfortunately the problem is rendered all the more difficult from the fact that the large series of specimens necessary for its solution are seldom available, so that characters may be considered of specific value, or . . . as mere abnormalities, when they are really normal variations, or perhaps, due to changes brought about by age." One needs, then, a reasonably large series of skeletons in order to determine the typical pattern of bony elements. Variation is found in all species of birds; it should be expected.

Shufeldt (1888:326) commented briefly on variation in the number of cervicodorsal ribs and Berger (1952:518; 1955a:587) on their uncinate processes. Lucas (1888, 1889, 1893) cited examples of variation in the numbers of true ribs. He stated (1888:52–53) that extra ribs are "not uncommon," but that "any lessening of the normal number is very rare and only once has such a case come under my notice," a Catbird (*Dumetella carolinensis*), in which the true ribs were reduced to five. Fisher (1946:562) discussed variation in the fenestration of the posterior margin of the sternum and stated that "in *Cathartes* the individual differences in fenestration are manifold."

In spite of the fact that Shufeldt and other earlier workers stated unequivocally, at times, that the several regions of the vertebral column contained a specific invariable number of vertebrae, Berger (1952, 1953, 1954, 1955a) presented evidence to the contrary. The number of cervical and dorsal vertebrae is relatively constant within cuculine genera. *Geococcyx, Crotophaga,* and *Chrysococcyx* (including "*Chalcites*" and "*Lampromorpha*") have 14 cervical vertebrae; to date I have found no variation in these genera. Thirty out of 31 specimens of the genus *Coccyzus* had 13 cervical vertebrae (contrary to the report by Shufeldt that this genus has 14), whereas the other specimen had 14 cervical vertebrae, certainly an anomalous number for this genus (see Berger, 1954:8–9). Of ten cuculine genera I have investigated thus far, I have seen only one example of variation in the number of dorsal ("thoracic" of some authors, but see Newton, 1896:849) vertebrae. The *Chrysococcyx* complex normally has four dorsal vertebrae. "One alcoholic specimen of *Chrysococcyx cupreus,* however, has five dorsal vertebrae and five dorsal, or true, ribs. Of the latter, four articulate with the sternum, while the fifth fuses ventrally with the fourth rib; there is no thoracic rib" (Berger, 1955a:

587). When the normal number of four dorsal vertebrae is present, there is also a thoracic rib. On the other hand, variation is common in the number of ribs which articulate directly with the sternum. With a total of 14 alcoholic and skeletal specimens for study, the following variation was found. "Four, apparently, is the 'normal' number of sternal ribs in these species. In one specimen of *Chrysococcyx cupreus* and two specimens of *Lampromorpha caprius*, however, only three of the four dorsal ribs articulate directly with the sternum; and in an alcoholic specimen of *L. klaas* three ribs articulate with the sternum on the left side, whereas four do so on the right" (Berger, *loc. cit.*).

I recently examined 14 skeletons representing six genera and nine species of Plantaineaters (Musophagidae). All except one had five dorsal vertebrae; one skeleton of *Turacus persa* (USNM No. 291,319) had but four dorsal vertebrae.

Two other regions of the vertebral column, however, exhibit considerable variation in the numbers of included vertebrae: the synsacrum and the free caudal vertebrae. Counting the fused vertebrae in the adult synsacrum is, at times, a difficult task. Moreover, no author, apparently, has told how he counted the individual vertebrae in the synsacrum; it is possible to count them in at least two ways so that one obtains two different answers. There is no doubt, however, that variation does occur. The following data are an example of such variation.

	Number of specimens			
No. of fused vertebrae in synsacrum	*americanus*	*Coccyzus* *erythropthalmus*	*Crotophaga sulcirostris*	*Geococcyx californianus*
11	15	3	4	22
12	40	10	2	2
13	2	....	....	....

Notwithstanding this variation, there is a preponderance of 12 fused vertebrae in the synsacrum of *Coccyzus* and of 11 in *Geococcyx*.

When one is dealing with articulated skeletons, there can be no doubt about the precise number of free caudal vertebrae. Intraspecific variation in the number of free caudal vertebrae is illustrated as follows:

	Number of specimens				
No. of free caudals	*americanus*	*Coccyzus* *erythropthalmus*	*Crotophaga sulcirostris*	*Geococcyx californianus*	*Coua caerulea*
4	....	....	2	....	1
5	39	11	3	20	2
6	18	3	1	2	1

In addition, Milne-Edwards and Grandidier (1879:170) reported that generally there are seven free caudal vertebrae in *Coua*, but recognized that there might be less than seven due to fusion of one or more with the pygostyle. In the musophagids mentioned previously, the number of free caudal vertebrae varied from five to seven. Burt (1930:477) found from five to seven free caudals in certain woodpeckers.

It would be superfluous to comment on intraspecific variation in length of the individual long bones of the appendages. Further detailed studies (Ashley, 1941) on the configuration of these bones, and of the amount of variation therein, however, would yield information valuable to the anatomist, taxonomist, and the paleontologist. The avian skull has been studied in great detail, but little has been published on variation in that structure (see Shufeldt, 1887).

It is not redundant to stress the value in having large series of completely articulated skeletons in order to determine the normal limits of variation in bony elements. With a box of disarticulated skeletal elements, how can one be sure that all of the cervical or free caudal vertebrae are present? Berger (1955b:302) commented: "Tabula-

tion of the number of fused vertebrae in the synsacrum (a difficult and, perhaps, unreliable determination in the adult bone) may be meaningless unless one also presents the numbers of cervical, dorsal, and free caudal vertebrae; the total number of bones in the vertebral column may be the same in two specimens of a species even though there may be variation in the numbers of vertebrae in adjacent regions." At the same time, in a report on three genera of American cuckoos, Berger (1952:519) found that "there appears to be no significant correlation between the number of fused vertebrae in the synsacrum and the number of free caudal vertebrae." Further data are needed on other groups of birds. It is certainly true that the number of free caudal vertebrae or the number of fused vertebrae in the synsacrum of a single specimen has little significance beyond reporting the condition in that specimen. Contrary to Shufeldt's assertion (1888: 332, 347), there is no justification for the statement, which appeared in a recent taxonomic paper, that "a diagnostic feature of the Corvidae" is the presence of 11 fused vertebrae in the synsacrum (Ripley, 1955:143). In the synsacra of 63 skeletons of corvids, representing 13 genera, I found that 42 synsacra each had 11 vertebrae and 21 had 12 vertebrae. For a recent discussion on skeletal variation in the Anseriformes see Verheyen (1953).

<div align="center">ANGIOLOGY</div>

It can be said with little fear of contradiction that the blood vascular system is the most variable system in the body. The reasons for this variability lie in the embryological development of that system.

Blood is carried to the upper extremity through a major channel, which, for purposes of description, is given different names in successive regions: the subclavian, axillary, and brachial arteries. At the elbow, the brachial artery typically divides into two terminal branches, the radial and ulnar arteries. Certain branches of this main stem have a distinctive course or supply particular structures; these branches are given specific names. There are many unnamed branches, referred to as muscular branches; they are variable in number and position. The definitive radial and ulnar arteries are preceded by other arteries in the human embryo which, each in turn, serve temporarily as the dominant arterial channel; these are the anterior interosseous, median, ulnar, and superficial brachial arteries. The anterior interosseous and the median arteries undergo retrogression and usually are small vessels in the adult. Most of the proximal portion of the superficial brachial artery degenerates. The antebrachial portion of this artery makes a secondary connection with the brachial artery near the elbow to form the definitive radial artery. Such an ontogenetic pattern in the development of the arterial system readily accounts for the variations or anomalies seen in the laboratory. One may find a very large, rather than a minute, median artery. The proximal portion of the superficial brachial artery may persist, so that either the radial or the ulnar artery appears to be a direct continuation of this trunk; or it may give rise to both the radial and ulnar arteries, in which case this division takes place high in the arm rather than at the elbow. An accessory ulnar artery may be present. These are but a few of the many examples which might be cited from human anatomy.

The important feature in the above discussion is that none of the variants represents wholly new channels: all were present as main channels or plexuses during embryological development. They are anomalies in the adult because normal retrogression, or allied processes, did not occur. In the development of an organism as elaborate as a bird or mammal, such minor deviations from a genetically established pattern are not very surprising.

For purposes of description, the subclavian artery is divided into three parts. Two cervical arteries, one from the first part, the other from the third part, supply the same

areas. Each of these two is said to have about 50 per cent occurrence; in some individuals both are present, although they are not usually the same size. One would not attempt to classify man on the basis of the presence or absence of these arteries, or on their relative size.

Developmentally, the aortic arches are bilateral structures. The definitive adult pattern of the aorta and the major arteries of the heart is the result of retrogression, shifting, and recombination of channels already present and the establishment of some new connections formed from pre-existing vascular networks. Essentially, one might say that nothing new had been added. Needless to say, many anomalies are encountered. The interested reader may consult Piersol (1930:724–726), Barry (1951), Woodburne (1951), and Patten (1953:632, 673).

I doubt that "the site of attachment of the intercostal or thoracic artery" in birds "may come to be used as an index in specific levels of evolution" or that "the medial migration of the thoracic artery appears to have some phylogenetic significance" (Glenny, 1955:543–544). Such variation is to be expected in the vascular system. In spite of the vast literature on the main arteries in the region of the heart, ornithologists still await the publication of a carefully executed paper describing the arterial and venous systems of birds. Names of arteries mean little if one cannot visualize their position. Such a paper should describe in detail the origin, course, relations, and destination of each artery (or vein), as in any text book of human anatomy. This treatment would be valuable and most welcome to all ornithologists interested in anatomy, because, among other things, it would serve as a basis for comparative studies.

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