THE PNEUMATIC FOSSA OF THE HUMERUS IN THE PASSERES

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ONE of the greatest hinderances to the successful unravelling of the interrelationships between passerine families is the shortage of morphological features varying sufficiently between these groups to be useful as taxonomic indicators. The search for potential taxonomic characters has concentrated largely on the skeleton, which is, in spite of other shortcomings, the easiest and most convenient anatomical material to collect and study. Except for some features used to divide the perching birds into suborders, almost all of the past anatomical-systematic work was based on skeletal characters, and indeed this work has rested almost entirely on cranial features. But, although the skull can and does provide many good clues to relationships between passerine birds, a shadow of doubt always hangs over the conclusions because of the convergence hazard resulting from similar feeding habits in unrelated groups. No matter how many different cranial features are employed, all may be functionally associated and thereby are under the influence of the same selection force; hence they should be considered as members of a single character complex (= functional complex or functional unit). Evaluation and comparison of the individual components of a character complex in taxonomic work is exceedingly difficult, and even when the greatest care has been used, the results may still be subject to question. In systematic work it is safest to consider a character complex (*e.g.*, the skull and associated structures) as a single unit or taxonomic character. It would, therefore, be most desirable to be able to check taxonomic conclusions based on cranial features by the use of postcranial skeletal characters; these latter structures are, in most instances, not directly influenced by feeding habits and hence do not belong to the same character complex as do the cranial features. Unfortunately, the postcranial skeleton is highly uniform throughout the Passeres except for differences in proportions and other minor features, such as variations in the number of the ribs and vertebrae. These proportional and numerical differences have little, if any, value in showing affinities between groups of perching birds. Any feature of the postcranial skeleton varying between passerine families is consequently of great importance to the student of avian classification as a potentially valuable taxonomic character.

The pneumatic fossa of the humerus is one of the few postcranial features exhibiting marked variation within the passerine birds. Although this variation was already known in the last century (Shufeldt, 1888), it has received little attention from avian anatomists. For example, it is not mentioned in the standard texts of Fürbringer, Gadow, and Beddard, nor

has it been used as a taxonomic character until quite recently. The first worker to stress the possible taxonomic significance of the pneumatic fossa was Ashley (1941), who studied its variation in the Corvidae. Ashley also commented on the variation of the pneumatic fossa throughout the Passeres and offered a functional explanation for this variation. His general conclusions were (1) that the single-fossa condition was primitive while the double fossa was more advanced, and (2) that families having the single fossa are more primitive than those possessing a double pneumatic fossa. More recently, Berger (1957: 240, 266–267) presented much additional data on the condition of the pneumatic fossa in many passerine families in connection with his investigation of the relationships of the starling genus *Fregilupus*, but the scope of his study prevented him from probing deeper into the functional and taxonomic meaning of this structure. Of significance is Wetmore's (1957; 1960: 21) use of the variation in the pneumatic fossa to arrange the oscine families into a linear sequence; those families with a single condition of the fossa were considered to be less advanced than those families with a double fossa. Wetmore thereby agreed with Ashley's major conclusions. This arrangement of the Oscines according to the condition of the pneumatic fossa is quite controversial, as shown by the divergent opinions of Delacour and Vaurie (1957: 3) and of Mayr (1957). In view of the disagreement on the taxonomic value of the pneumatic fossa and because of its potential importance in the classification of the Passeres, I would like to review the available evidence, using the concepts of the "single character study" method (Bock, 1960, especially, pp. 363–364, 478–479) as a means of ascertaining what is already known and what must still be learned before the "taxonomic value" of the pneumatic fossa can be determined.

Description of the Pneumatic Fossa of the Humerus

The species to be described below were chosen as examples of the two major conditions of the pneumatic fossa, and of several intermediate stages

between them. In all cases, the right humerus will be described and illustrated. The terminology of Ashley (1941) is adopted for the parts of the humerus.

The humerus of the jackdaw (*Corvus monedula,* Figure 1A) is typical of the single-fossa condition. The fossa lies directly distal to the internal tuberosity and posterior to the medial bar. Posteriorally, the pneumatic fossa is bordered by the bicipital crest, which continues into the shaft of the humerus in a smooth, shallow curve. The limits of the fossa, especially medially and distally, are not sharply defined but merge gradually into the shaft of the bone. At the proximal end of the fossa, the opening (pneumatic canal) into the hollow interior of the humerus with its system of bony struts or trabeculae can be seen. The surface of the humerus between the anterior (medial) border of the pneumatic fossa and the capital-shaft ridge is smooth; there is no hint of a second, more anterio-proximal fossa. The posterior edge of the capital-shaft ridge is only slightly raised above the surface of the humerus lying between the ridge and the pneumatic fossa.

The starlings of the genus *Eulabes* (Figure 1 C) show a beginning stage in the development of the second, more anterio-proximal fossa. The original pneumatic fossa lies in the same position as in the jackdaw, but it is deeper and more sharply delimited from the rest of the bone. Just distal to the head of the humerus and posterior to the capital-shaft ridge is a slight depression, which represents the beginning of the second fossa. Note that there is no connection between the original pneumatic fossa and the second concavity. With the appearance of the new concavity, the posterior edge of the capital-shaft ridge has become more elevated above the surface of the bone just posterior to it than in the jackdaw, and is much more sharply defined. The internal tuberosity is shifted a bit posteriorally and is at a greater angle to the shaft of the humerus, with the result that it hangs over the pneumatic fossa more than in the jackdaw. With the shift of the internal tuberosity, the bicipital crest is bent distally so that it meets the shaft of the humerus at a greater angle.

The next stage in the development of the double-fossa condition is shown by the starlings of the genus *Sturnus* (Figure 1D). The second, more proximal concavity has enlarged to become a quite distinct fossa with a deeper depression extending under the head of the humerus; but the second cavity is still completely separated from the original pneumatic fossa by the well-developed medial bar. The capital-shaft ridge extends well above the bone posterior to it and has a very distinct posterior edge. Indeed, the posterior face of the capital-shaft ridge is perpendicular to the floor of the second fossa, which lies immediately behind it. The pneumatic
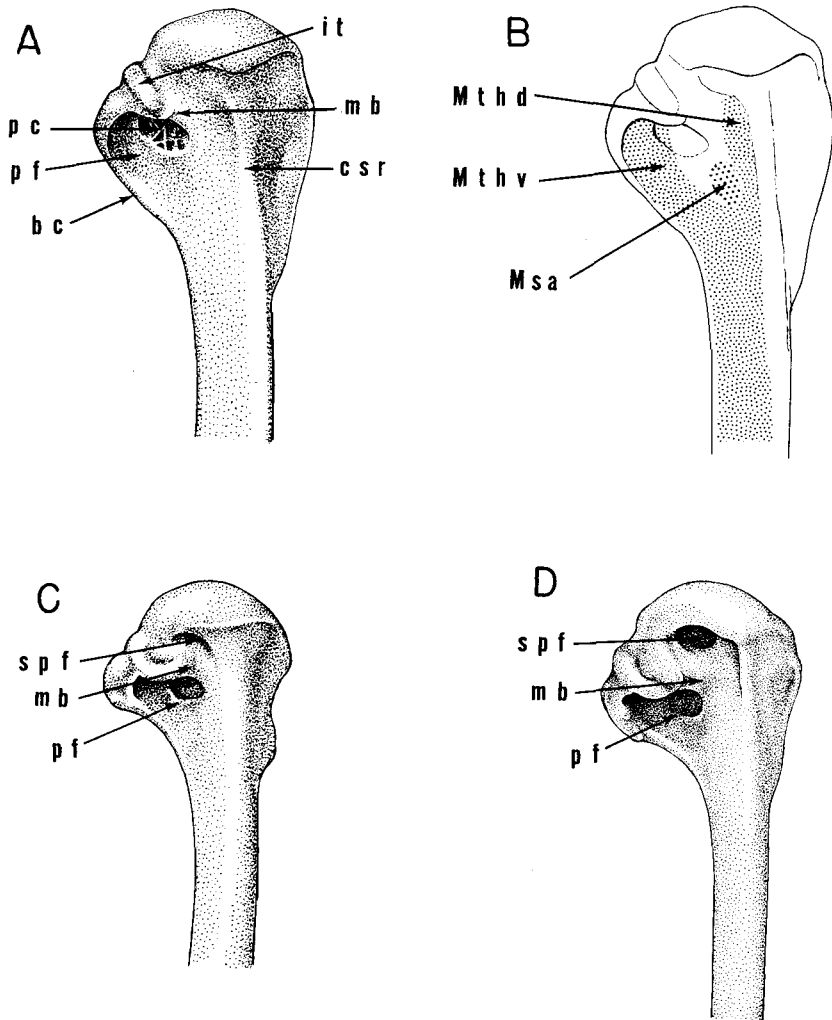
Figure 1. The right humerus of (A) *Corvus*, (C) *Eulabes*, and (D) *Sturnus*
to show the pneumatic fossa. Note that the second pneumatic fossa begins its
development as a concavity beneath the head of the humerus and is sepa-
rated from the original pneumatic fossa by the medial bar. The abbreviations
used are: bicipital crest (b c), capital-shaft ridge (c s r), internal tuberosity
(i t), Medial bar (m b), pneumatic canal (p c), pneumatic fossa (p f), and
second pneumatic fossa (s p f). The attachments of the muscles associated
with the pneumatic fossa in *Corvus* are shown in Figure B. The fine stippling
indicates the origins of the dorsal (m t h d) and the ventral (M t h v) heads
of the M. triceps humeralis. The heavy stippling indicates the insertion of
the M. scapulohumeralis anterior (M s a), which is located at the distal end
of the pneumatic fossa. The figures are not drawn to scale.

fossa, internal tuberosity, and bicipital crest are much the same as in *Eulabes.*

In the thrushes (*Turdus,* Figure 2A) the second fossa is larger than in *Sturnus,* with the head of the humerus being deeply excavated. The capital-shaft ridge is still further developed over the *Sturnus* condition with a well-defined posterior wall. The two fossae may be considered to have merged into a single structure, although the medial bar is still strongly developed and forms a wall separating the original pneumatic and the second fossae into two quite distinct halves. The internal tuberosity, pneumatic fossa, and bicipital crest are all quite similar to the *Sturnus* condition; but it can be easily seen that the original pneumatic fossa is relatively much larger and better defined than the fossa in the jackdaw, and that the bicipital crest meets the shaft of the humerus at a greater angle (almost at a right angle).

The hawfinch (*Coccothraustes,* Figure 2C) shows the final stage in the development of the double pneumatic fossa. The condition of the second fossa and of the capital-shaft ridge is much the same as in the thrushes. However, the two fossae are now fully joined with the reduction of the medial bar to a small ridge along the proximal wall of the now double pneumatic fossa. In the final stage, the double fossa occupies the entire space between the bicipital crest and the capital-shaft ridge, with the proximal part of the original pneumatic fossa as well as the second fossa being deeply excavated into the internal tuberosity and the head of the humerus. The shape of the bicipital crest is the same as in the thrushes.

It should be emphasized that the double fossa condition develops by the appearance of a second concavity just distal to the head of the humerus and the subsequent development of this concavity (as already described by Ashley, 1941, and Berger, 1957). The two fossae do not meet and merge into one another until after the second fossa is fully developed. Merging of the fossae occurs by the reduction of the medial bar. The double-fossa condition does not develop by the enlargement of the original pneumatic fossa toward the head of the humerus as might be interpreted from Wetmore's description (1957) of the double fossa in the nine-primaried Oscines.

OCCURRENCE AND VARIATION OF THE PNEUMATIC FOSSA

Ashley reported the double fossa from the New World nine-primaried Oscines, the Ploceidae, and some members of the Mimidae, and mentioned the single condition in several oscine families, such as the Corvidae and the Hirundinidae, and in some suboscine groups; however, he did not present a thorough survey of the variation of this structure throughout the entire order. Nor did Wetmore describe the variation of the pneumatic
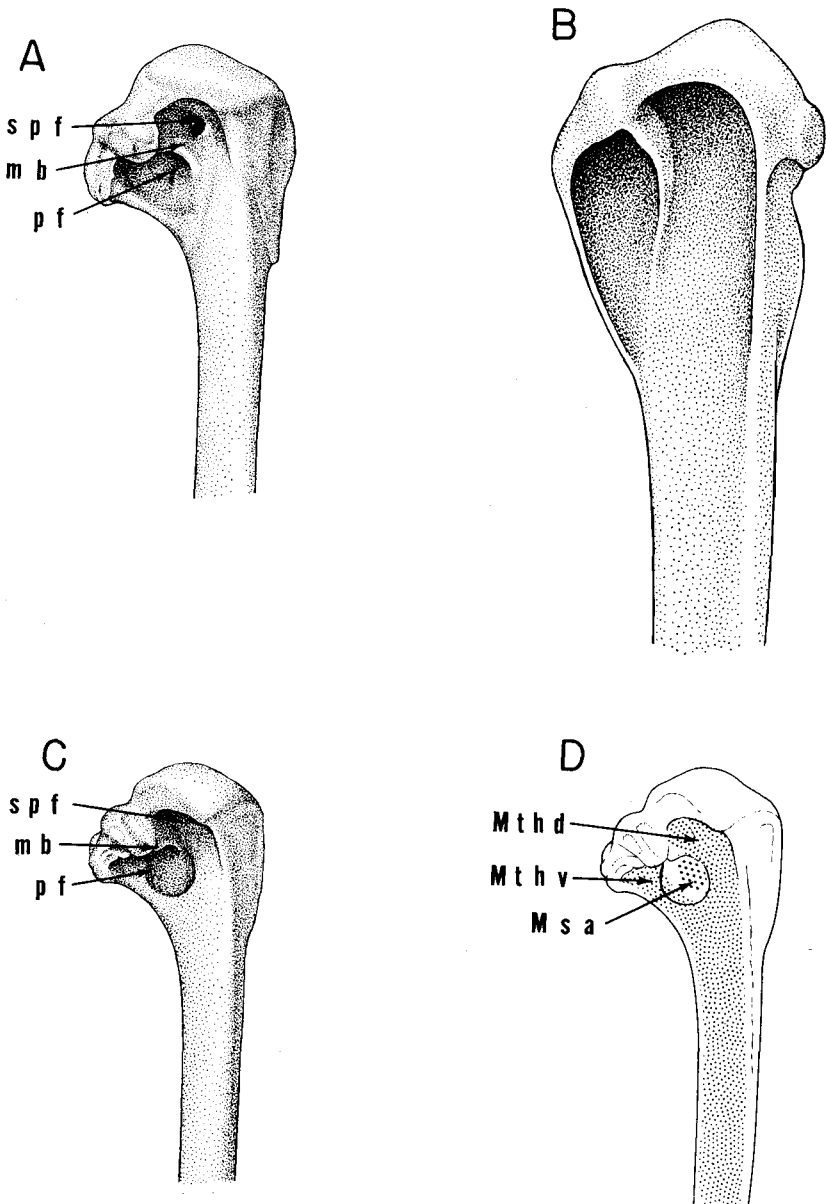
Figure 2. The right humerus of (A) *Turdus*, (B) *Larus*, and (C) *Cocco-thraustes* to show the pneumatic fossa. Note that in both *Turdus* and *Cocco-thraustes*, the fossa is doubled, but that in *Turdus*, the medial bar is well developed while it has almost disappeared in *Coccothraustes*. In *Larus*, the double fossa is oriented along the longitudinal axis of the humerus and is

fossa throughout the Passeres. Berger (1957: 266–267) reported the condition of the fossa in many passerine families; but, although his survey is the best to date, it is still not complete. To supplement the data provided by these workers, I have examined the pneumatic fossa in the Passeres and in the several orders usually placed near them in recent classifications. In this survey, I have tried to obtain a good picture of the condition and variation in each family; however, no attempt was made to examine every genus available or to ascertain the exact details of the structure and variation in each family. The results of this rough survey shall be presented in a most abbreviated manner; such details as the genera and the number of specimens examined will be omitted. Suffice to say that a good representative sample was seen of all but the rarer families. To report this survey in greater detail would be superfluous because of the lack of knowledge of the functional aspects of this problem. Indeed, the morphological details, rough as they may be, are far finer and more precise than the functional information available at present.

Among the nonpasserine orders I have examined specimens of the Coliidae, Trogonidae, Alcedinidae, Todidae, Momotidae, Meropidae, Coraciidae, Upupidae, Bucerotidae, Galbulidae, Bucconidae, Capitonidae, Indicatoridae, Raphastidae, and Picidae. The pneumatic fossa is single (undivided) in all families except for the Todidae and the Indicatoridae. In the Todidae the fossa is double (divided), while in the Indicatoridae the second fossa is developing and has already reached a well-formed state. It must be emphasized, however, that I was able to examine only relatively few specimens of both families and that more material must be examined before these observations on the condition of the fossa in the Todidae and the Indicatoridae can be accepted as conclusive.

Among the suboscine passerine families I examined the Eurylaimidae, Dendrocolaptidae, Furnariidae, Formicariidae, Conopophagidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae, Phytotomidae, Pittidae, and Menuridae. The pneumatic fossa is single in all groups.

In the Oscines the variation of the pneumatic fossa is rather complicated and is difficult to describe briefly, but it is hoped that the following description will be clear enough for the purposes of the present study. The sequence of oscine families to be used in *Peters' Check-list* shall be

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quite unlike that seen in the passerine birds. The attachments of the muscles associated with the pneumatic fossa in *Coccothraustes* are shown in Figure D. Note that the dorsal head of the M. triceps humeralis is larger than in *Corvus* and that the insertion of the M. scapulohumeralis anterior is located closer to the head of the humerus and lies in the distal end of the second pneumatic fossa. All abbreviations are as in Figure 1. The figures are not drawn to scale.

followed. In the Alaudidae and Hirundinidae the second fossa is developing, with *Progne* being furthest advanced toward the double condition. The Motacillidae exhibit the double condition. The second fossa is developing in the Campephagidae (almost completely doubled in *Pericrocotus*) and in the Pycnonotidae (best developed in *Phyllastrephus* and *Calyptocichla*). In the Irenidae (hint of the second fossa in *Aegithina*), Laniidae, and Bombycillidae (including *Dulus*) the fossa is single. The Cinclidae show the double condition. In the Troglodytidae the second fossa is forming with the greatest development in *Heleodytes*. The two-fossa condition is present in the Mimidae, Prunellidae, and Turdinae (including *Zeledonia*), but the double condition is only developing in the Timaliinae (best in *Malia, Yuhina, Gampsorhynchus,* and *Chamaea*), the Sylviinae (completely double in *Regulus*), and the Muscicapinae. In the Paridae (especially well developed in the smaller forms), Sittidae (*Sitta* and *Rhabdornis,* but not in *Hypositta* in which the fossa is single), Certhiidae (including *Tichodroma*), Dicaeidae, Nectariniidae, and Zosteropidae the fossa is double. But in the Meliphagidae the second fossa is developing with a well-developed double fossa in *Conopophila,* but a poorly developed one in *Philemon.* In the entire New World nine-primaried Oscines except for the Vireonidae and a few other genera the fossa is doubled. The Vireonidae exhibit only the beginnings of the second fossa. It should be noted that in the larger genera of the Icteridae, the second fossa is very small or absent as already reported by Berger. The Fringillidae, Estrildidae, Ploceidae, and Sturnidae (most genera) possess a double fossa, while the Oriolidae, Dicruridae, Grallinidae, Artamidae, Cracticidae, Ptilonorhynchidae, Paradisaeidae, and Corvidae have a single fossa. Members of a number of smaller families, such as the Prionopidae and the Callaeidae, were not readily available, but their omission from the survey is of little importance at this stage in our knowledge. It should be noted that there is very close agreement between the results reported by Ashley, Wetmore, and Berger and my observations.

The general pattern of variation is the single-fossa condition in the non-passerine orders and in the suboscine passerines. In the Oscines the pneumatic fossa exhibits an almost meaningless pattern of variation. Part of this random pattern may be an artificial result of the sequence used. If the crowlike and the shrikelike families are placed together, as done by Amadon (1957) to form his Group 1 (but minus the Alaudidae and the Hirundinidae), these families agree in that almost all have the single condition of the pneumatic fossa. Among the other oscine birds the general trend is toward the development of the second fossa with a fully developed doubled condition present in many diverse lines. The New World nine-primaried Oscines appear to be the only larger subgroup

within the Oscines, that is rather uniform in having a fully developed double condition.

FUNCTIONAL ASPECTS OF THE PNEUMATIC FOSSA

Ashley (1941: 193) suggested that the development of the double condition of the pneumatic fossa may be associated with increase in size of the medial branch of the M. humerotriceps (= dorsal head of the M. triceps humeralis) and postulated that the increase in strength of this muscle is correlated with the ability of vertical flight. Although parts of his discussion are sound, others are oversimplified or not substantiated (this is especially true for the statements on flight), and his study introduces more problems than are solved. Therefore, the entire question of the functional meaning of the pneumatic fossa and of its modifications shall be discussed. It is necessary to describe first the muscles associated with the pneumatic fossa; these are the M. triceps brachii and the M. scapulohumeralis anterior. I shall describe and compare these muscles in a bird with a typical single fossa and in a bird with a well-developed double fossa. The extension of the interclavicular air sac that enters the hollow interior of the humerus through the pneumatic canal does not appear to be responsible at all for the evolution of the double-fossa condition. The second fossa is a blind concavity on the surface of the humerus without any connection to the hollow interior of the bone. The terminology for the muscles is taken from Hudson and Lanzillotti (1955), to which the reader is referred for a description of the entire pectoral musculature.

In *Corvus* (Figure 1B) the humeral portion of the M. triceps brachii, the M. triceps humeralis, originates from the humerus by means of two heads. The ventral head originates from the pneumatic canal and the posterior wall of the pneumatic fossa and then from the shaft of the humerus where it merges with the dorsal head. The dorsal head originates along the posterior side of the capital-shaft ridge starting from a point just proximal to the medial bar; again the origin extends down the shaft of the bone until it merges with the origin of the ventral head. The two heads of the M. triceps humeralis are separated by the insertion of the M. scapulohumeralis anterior. They join distal to this muscle, and the now united M. triceps humeralis originates from the entire shaft of the humerus to a point just above the distal condyles. The two heads of the M. triceps humeralis are subequal in size. The second muscle associated with the pneumatic fossa, the M. scapulohumeralis anterior, originates from the anterior end of the scapula and inserts between the two heads of the M. triceps humeralis on the anterior edge of the pneumatic fossa just distal to the medial bar. This small, narrow, and bandlike muscle

lies deep in the shoulder region, hence preserving poorly and tearing easily as one manipulates the wing in order to obtain a better view of the muscle and its attachments. The exact course of the muscle is difficult to follow, and indeed in any one specimen the observed course depends largely upon how the wing was placed during initial preservation. Nevertheless, the general course of the M. scapulohumeralis anterior is through the capital groove and over the distal end of the medial bar, after which the muscle reaches its insertion.

In the hawfinch, *Coccothraustes* (Figure 2D), the size and attachments of these muscles are somewhat modified. The ventral head of the M. triceps humeralis is much the same as in *Corvus*, but the dorsal head is larger and originates from the entire area of the second fossa. Therefore, the origin of the dorsal head extends more proximal and covers a larger area than in *Corvus*; the M. triceps appears to be relatively more powerful in the hawfinch than in the crows. The M. scapulohumeralis anterior originates from the anterior end of the scapula, but its insertion appears to be more proximal and anterior than in *Corvus* so that it lies within the second fossa and closer to the head of the humerus. The excavation of the head of the humerus associated with the development of the second fossa has resulted in a deeper insertion of the M. scapulohumeralis anterior in that bone. The muscle is therefore longer, and its origin and insertion present a quite different relationship to one another than in birds having an undivided fossa; the result is that the action of the M. scapulohumeralis anterior in rotating the humerus in the hawfinch appears to be different than in *Corvus*.

It is possible to describe the actions of these muscles in the method of classical descriptive anatomy (see Hudson and Lanzillotti, 1955, for this information), but the major problems are (1) the actual function of these muscles during flight, and (2) how the differences in the positions of the muscle attachments in the single- versus the double-fossa conditions affect the function of the muscles and the flying ability of the birds. Unfortunately, our knowledge of avian flight is insufficient to answer these questions or even to guess at a plausible answer. I have made a search through the literature on avian flight (Sy, 1936; Stolpe and Zimmer, 1937, 1939; Steinbacher, 1960) and have found nothing dealing with the functions of the individual pectoral muscles (aside from some simple comments on the M. pectoralis and the M. supracoracoideus—the flight muscles) during flight. All of the earlier studies on avian flight have dealt either with the action of the wing as a unit or with the structure and proportions of the skeletal elements. Even Sy's extensive work on the wing muscle does not go into the functions of the individual muscles, especially the smaller muscles during flight. Sy gives no information on the M.

scapulohumeralis anterior other than describing it briefly. And there is
no existing experimental work pertinent to this problem. Thus it is not
possible to progress further into the question of the function of the muscles
associated with the pneumatic fossa or into the functional meaning of the
development of the double-fossa condition. But before leaving this part
of the problem, it is necessary to review Ashley's functional conclusions,
although it should be pointed out that it is not possible to verify or dis-
prove them.

Ashley concluded that the development of the second fossa is correlated
with increase in the size of the dorsal head of the M. triceps humeralis.
Enlargement of the M. triceps would serve to extend the forearm more
powerfully; an action that, Ashley claimed, is essential for vertical flight.
This correlation appears to be far too simple and is questionable for two
main reasons. First, a fully developed fossa is present in many passerine
birds that do not fly vertically, as pointed out by Wetmore (1957).
Second, the development of the second fossa involves an entire reorganiza-
tion of the palmar surface of the humerus posterior to the capital-shaft
ridge; this reorganization affects the action of the M. scapulohumeralis
anterior as well as the M. triceps humeralis. Modifications in the actions
of both muscles must be considered simultaneously. Yet the problem is
more complicated. Although the actions of both muscles appear to be
different when one compares birds possessing the single-fossa condition
with those having the double-fossa condition, it is not necessary to assume
that both muscles began their evolutionary change at the same time and
have then evolved simultaneously. It seems more likely that change in one
muscle occurred first, which must therefore be considered as the factor
responsible for the origin and evolution of the second pneumatic fossa.
If this is the case, change in the other muscle may have occurred as a
consequence of the evolutionary change in the first muscle. Although the
reasons for the following opinion are highly speculative, it seems possible
that a shift in the insertion of the M. scapulohumeralis anterior to permit
a different turning action by this muscle on the humerus was the original
evolutionary step—the one responsible for the development of the second
fossa. In spite of the small size of this muscle, its action rotates the
humerus and thereby the entire wing; a slight shift in its insertion could
result in a great functional change. The difference between the insertion
of the M. scapulohumeralis anterior in the crow and in the hawfinch sug-
gests that its rotative action on the humerus is quite different in the two
forms. Because the muscle is very short and because its attachment is
close to the proximal articulation of the humerus, an excavation of the head
of the humerus to form a deeper attachment seems to be the most plausible
way to achieve a significant shift in the insertion of the M. scapulo-

humeralis anterior. This excavation could lead to the observed reorganization of the head of the humerus—the development of the double-fossa condition. The other possibility is that increase in size of the dorsal head of the M. triceps humeralis was responsible for the origin of the second fossa as has been suggested by Ashley. In this case, the need for a more powerful extension of the forearm would be met by an increase in the size of the entire M. triceps. It is difficult to understand why need for a more powerful extension of the forearm would lead to an increase in size and length of only the dorsal head of the M. triceps humeralis and hence to the origin and development of the second fossa. The muscle could achieve the necessary increase in strength by an increase in the number of muscle fibers through altering its internal construction, *i.e.*, by becoming pinnate, or by increasing the mass of all parts of the M. triceps brachii. Increase in length of the muscle (which is only a minor increase, less than 10 per cent of the original length) or an extensive reorganization of the humeral head to provide a greater area of origin for the muscle, both of which have been suggested by Ashley, is not necessary to increase the strength of this muscle. The main theoretical objection to Ashley's suggestion, although it is a possible explanation and has some evidence in its favor, is that the morphological changes to be explained are quite complex in comparison with the changes in function and with the selective demands on this muscle-bone system that Ashley uses as the basis for his explanation. Usually in evolution, an environmental demand upon an animal is met by the simplest possible morphological modifications for the needed functional changes. Yet in the course of evolutionary change, the simplest modification from the human viewpoint is not always the one that has occurred, but it is the one for which the necessary genetical factors have appeared. But there is little sense to speculate further on this problem. What is needed first are detailed studies on the precise function of the wing muscles during flight, and then to ascertain the correlations between the muscle structure and function with the structure of the pneumatic fossa in a number of passerine species. Here is an untouched area of investigation, albeit a most difficult one, for the functional anatomist. Nevertheless, besides being of upmost importance to the solution of the functional significance and evolution of the pneumatic fossa, studies into the precise function of the wing muscles would have a bearing on many general problems of functional anatomy and evolution, and the results should more than repay the efforts.

Discussion

The available information about the pneumatic fossa of the humerus may be summed up as a fairly good knowledge of its structure and varia-

tion in the Passeres and related orders as well as knowing which muscles appear to be functionally correlated with it. We do not know the function of this bone-muscle system during bird flight or the significance of the change from the single- to the double-fossa condition, nor do we have any idea of the evolutionary history of the fossa. Using the available data and considering what we do not know, I would like to discuss the major conclusions regarding the pneumatic fossa reached by earlier workers. These conclusions are: (1) that the primitive condition is the single fossa and the advanced condition is the double fossa; (2) that birds with a single pneumatic fossa are primitive, while those with a double fossa are advanced; and (3) that the pneumatic fossa is a good taxonomic character in the Passeres.

All of the earlier workers agree that the primitive form of the pneumatic fossa in the Passeres is the single condition. This conclusion is supported by the fact that the single fossa is the simpler condition structurally and by the distribution of the fossa conditions in birds. Most birds, including the nonpasserine orders, the suboscines, and many oscine families, most of which are unspecialized and nonderived groups, have a single pneumatic fossa. A developing or a well-developed second fossa is present only in a number of oscine families (with the possible exceptions of the todies and the honey-guides), many of which are only distantly related to one another, and most of which are clearly derived and specialized groups. If the primitive form of the pneumatic fossa was the double condition, it would be difficult, if not impossible, to explain why it is found today only in some of the more advanced oscine families.

Following the conclusion that the primitive condition was the single fossa, it was assumed by Ashley that the single fossa is always primitive and that the double fossa is always advanced, and consequently that birds with a single fossa are primitive while those with a double fossa are advanced. Wetmore used this assumption as a basis for his conclusion that the pneumatic fossa can serve as an aid in the arrangement of the oscine families. Subsequently, Mayr has questioned the validity of this conclusion and the underlying assumptions. The major question, as mentioned by Mayr, does not lie in whether the primitive condition of the pneumatic fossa is the single fossa, but whether the single pneumatic fossa is always originally primitive, or whether it could not be secondarily simplified in some groups.

It may also be noted that the presence of a single primitive character or character complex does not prove that a given genus or family needs to be primitive in all other characters or that it must be considered to be primitive by being placed early in a sequence of taxa. Even if it could be shown that certain families are primitive with respect to the structure of

the wing (*e.g.*, the pneumatic fossa of the humerus) or the foot, they might not be primitive in other respects. This problem is especially acute in the Passeres in which the phylogeny could be better represented by a spreading flat-topped bush than by a tall Lombardy poplar.

If the last possibility actually exists, then the original assumption of Ashley cannot be accepted as completely correct. Unfortunately, our lack of knowledge of the functional aspects of the pneumatic fossa prevents us from speculating on the evolution of the double condition and the possibilities of reverse evolution from the double condition to a secondary single fossa. Yet one bit of evidence is available that does indicate that the single-fossa condition can be secondarily evolved. Berger (1957: 267) reports that in the emberizine genera *Passerherbulus* and *Ammospiza* the second fossa is very small so that these genera approach the single-fossa condition in contrast to the well-developed condition usually found in this family. Similarly, although most members of the Icteridae possess a well-developed double fossa, some of the larger genera (*Gymnostinops*, Berger, 1957: 267, and confirmed in my survey) have only a single pneumatic fossa. The Emberizinae and the Icteridae are members of the New World nine-primaried Oscines that are uniform in having a well-developed double fossa (except in some of the "ancestral" Vireonidae, which show the first rudiments of the second fossa). Thus the ancestors of the *Passerherbulus, Ammospiza,* and *Gymnostinops* had, in all probability, a well-developed double fossa; and, hence, the presence of a poorly developed second fossa or its complete absence (in *Gymnostinops*) constitutes a case of reverse evolution.[1] Among the other oscine families it is impossible to determine at this time if the observed single fossa is the original primitive condition or if it is a secondarily simplified structure. Therefore, it must be emphasized that the double assumption that the single fossa is always primitive while the double fossa is always advanced and hence that the fossa condition is a good indicator of the phyletic advancement of a passerine family has not been proved and thus cannot be accepted as an established fact. And although there is little direct evidence

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[1] These observations must be checked to insure that the observed single condition of the pneumatic fossa in these genera is the fully developed adult condition. Ashley (1941: 193) noted that in young individuals of *Agelaius phoeniceus*, an icterid, only the original pneumatic fossa is present, while in adults, the double-fossa condition is found. Thus, it is possible that in birds with a double condition as adults, the young have only the original pneumatic fossa. Consequently, it is possible that the differences reported by Berger are age variations—the examined specimens of *Passerherbulus*, etc., being young individuals. A careful investigation of the ontogeny of the pneumatic fossa, especially the establishment of the age at which the second fossa is fully developed, is needed before the full significance of Berger's observations can be ascertained. However, it seems most probable that the observed single-fossa condition in *Gymnostinops* is the adult condition, as the specimens examined by Berger and myself came from different museums and it is rather unlikely that, in both cases, the examined specimens were young birds.

arguing against this assumption, it would be best dropped from usage until more data bearing upon it have been gathered.

Here may be the best place to comment on the humerus of the gulls (*Larus*). The "double pneumatic fossa" in these birds has been cited both as evidence supporting the idea that the double fossa is advanced (because primitive gulls had a single fossa) as well as the fact that the double fossa can be found in "lower groups of birds," and hence that the presence of the double fossa does not necessarily indicate an advanced group of birds. Actually, the humerus of the gulls has nothing to do with the question of the double fossa in the Passeres. Comparison of the humerus of the gull (Figure 2B) with that of the Passeres will show that the basic construction of the head of the humerus is quite different in the two groups. In the gull the fossae are long and oriented along the long axis of the bone with a long, bladelike wall separating the two fossae in contrast to the short fossae lying at an angle to the long axis of the humerus in the Passeres. From the structure of the "double-fossa" condition in the gulls and in the passerines, it seems reasonable to assume that the muscles attaching to the fossae in the two groups have different functional relationships to the structure of the fossa and have evolved because of different selective demands on the birds. Thus, the earlier references to the gull humerus are meaningless to the present discussion and would be best omitted in future considerations.

The last conclusion, that concerning the taxonomic value of the pneumatic fossa, is the most controversial of all. Ashley, Wetmore, and Delacour and Vaurie concluded that the pneumatic fossa provides a good clue to the relationships within the Oscines, while Mayr questioned its value. Yet the information needed to evaluate the taxonomic importance of this character is lacking. It is my belief that a knowledge of the selection forces acting on a structure is absolutely essential before the taxonomic significance of that structure can be evaluated (see Bock, 1958: 31, 51–53; 1960: 364, 470). Roughly, it may be said that the taxonomic usefulness of a structure varies inversely with the changeability of the selection forces acting upon it, that is, the number of times the selection forces have reversed their direction or have arisen anew during the evolution of a group. Before the nature of the selection forces operating on a structure can be judged, one must first know the function of that structure and have some idea about its evolution. This information is lacking for the pneumatic fossa of the humerus, and, hence, in my opinion, its taxonomic usefulness cannot be assessed at this time.

It is still necessary to inquire deeper into the reasons behind Ashley's and Wetmore's conclusions that the pneumatic fossa is a valuable taxonomic aid in the Passeres. In their comparisons they contrasted the crow-

like birds having a typical single pneumatic fossa with the New World nine-primaried complex that have a well-defined double fossa. All of the other passerine families were more or less not considered. To contrast the crows and the nine-primaried Oscines, and to claim that there is a gradual transition through the Oscines from the single fossa in the crows to the double condition in the nine-primaried Oscines (Ashley, 1941: 193), is overly simplified and misleading. The variation of the pneumatic fossa in the Oscines does not show a simple, gradual change from the crows to the nine-primaried group, but a picture of apparently independent acquisition of the double condition in many different evolutionary lines. The degree of development shown by the second fossa in these lines varies from the slightest indication of the new fossa to a fully developed structure as found in the Motacillidae, Mimidae, Turdinae, Paridae, Sittidae, Dicaeidae, Nectariniidae, and others in addition to the nine-primaried complex. These families surely belong to a number of independent lines, and, on the basis of the pneumatic fossa, each of these families is fully as advanced as the members of the nine-primaried Oscines. The presence of the second fossa in many independent lines within the Oscines distracts from the usefulness of this structure as a taxonomic aid. The double pneumatic fossa cannot, therefore, be used by itself as proof that the New World nine-primaried Oscines are the most advanced or progressive members of the Oscines. There is, on the other hand, one interesting aspect of this polyphyletic development of the double-fossa condition that I have not considered in this paper, namely, whether the second fossa is always achieved in the same way and hence whether it is uniform in structure. Available evidence indicates that variation exists within the double-fossa condition, as, for example, in the degree of suppression of the medial bar (see Berger, 1957: 267), which can be well developed or almost absent. A more detailed study into the exact structure of the pneumatic fossa and the associated muscles may reveal additional characters of greater taxonomic importance than the simple single- versus double-fossa dichotomy.

Lastly, I would like to comment upon the statement by Wetmore (1957: 208) that: "The form of the head of the humerus is not subject to stresses which might cause modifications with any of the usual changes in type of food, habit, or habitat that appear to have affected the form of such structures as the bill and the feet, with their supporting bony framework. It remains the same in related groups, regardless of whether the method of flight is strong and direct, like that of a grackle, or weaker and undulating, like that of the cardinal already mentioned. The meadowlark alternately flits the wings rapidly and sails, resembling its relative the grackle. Even the swifts, highly modified for rapid flight, show no marked departure from related groups in this portion of the humerus. It must be

evident, therefore, that there is here a character of phylogenetic signifi-
cance, of value in judging close relationship, and useful as a detail in
arranging the levels of classification." Wetmore is correct in pointing out
that the functional meaning of the single versus the double fossa probably
has a complicated basis, but he touches upon a more significant topic. If
I interpret his comments correctly, Wetmore implies that the condition
of the pneumatic fossa is nonadaptive and is, therefore, valuable for sys-
tematic studies. Mayr (1958: 194) also distinguishes between functionally
important and taxonomically useful characters in saying: ". . . there is
always a hint that the real significance of the character is functional
rather than phyletic. . . ." The same conclusion is frequently made that
nonfunctional or nonadaptive characters (usually no difference is made
between these properties of a character) are the only useful taxonomic
features, or that their taxonomic usefulness is far greater than functional
or adaptive features (see, for example, Starck, 1959: 50–51, 57). First,
I wish to point out that because we have not yet deduced the adaptive
nature of the pneumatic fossa, including the functional meaning of the
observed modifications, this does not mean that this feature is non-
adaptive and, moreover, that it cannot readily change from one condition
to another with modifications (and even with slight modifications) in the
environment demands on the bird. But, more importantly, I would reject
completely the notion that a distinction exists between functionally im-
portant and taxonomically useful features, and that nonfunctional or non-
adaptive characters are more useful than functional or adaptive ones.
There is no basis for this concept, nor is there any need for it. It may be
pointed out that many (most or all?) of the nonadaptive features in birds,
e.g., the hallux in many groups, are vestigial[2] features and have little
taxonomic value (see Mayr, Linsley, and Usinger, 1953: 122, for a dis-
cussion of the taxonomic value of vestigial features). Actually it is useless
to make a distinction between taxonomically useful characters and adaptive
features because essentially all, if not all, of the taxonomic characters used
in avian systematics are functional and adaptive features. I cannot think
of a single taxonomic character in use in avian systematics today or dur-

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[2] The use of "vestigial" and "rudimentary" in biology is sometimes confusing,
especially when the English and German literature is compared. The most common
usage in the English language literature, which I shall follow, is as follows: (1) rudi-
mentary is used for structures that have just appeared in a phylogenetic or ontogenetic
sense and are poorly developed morphologically and functionally, and may become
better developed; while (2) vestigial is used for structures that are presently poorly
developed morphologically and functionally, and have evolved or developed from a
previously well-developed structure. In the German biological literature "Rudiment"
and "rudimentär" are used in the sense of the English "vestige" and "vestigial," not
in the sense of the English "rudiment" and "rudimentary" (as for example, see Starck,
1959: 49, footnote and under heading "a"). There is no commonly used equivalent for
the English "rudiment" in German biology.

ing the past that is nonfunctional and nonadaptive. Thus, the fact that modifications of the pneumatic fossa have, in all probability, an important functional basis does not detract in the slightest from its possible taxonomic value; this is dependent upon completely different factors.

SUMMARY

The pneumatic fossa of the humerus exhibits a considerable degree of variation within the Passeres and may be a potentially valuable clue to the interrelationships of the passerine families. But, at present, little is known about the functional meaning of the fossa and of the evolutionary changes from the single-fossa condition to the double-fossa condition, and it is not possible to ascertain the taxonomic value of the pneumatic fossa at this time. It is, therefore, recommended that the pneumatic fossa be used with great caution in passerine systematics until more has been learned about its function and evolution.

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