WING SKELETON AND FLIGHT OF HAWKS

BY WILLIAM L. ENGELS

SOME years ago Hans Böker (1927) attempted to show that each type of flight exhibited by birds is accompanied by a particular and precise pattern of proportions within the wing skeleton; and further, that the phylogenetic development of the flight types could be analyzed by comparative anatomical and ontogenetic study of these patterns. This pioneering work in an essentially new field of ornithological research (biologische Anatomie) seems not to have gained, outside of Germany, the recognition it deserves, perhaps due in some measure to a strongly Lamarckian flavor in its presentation. More recently Böker (1935) has elaborated his original schema and definitions of types.

In evaluating Böker's data, two questions arise. First, since he had at his disposal, at most, scanty material for each form, can one be certain that the proportions as illustrated by him are truly representative of the species concerned? Second, are the differences in proportion between types based on functional differences or are they primarily phylogenetic in origin?

With regard to the first question I have recently shown (Engels, 1938a), in a statistical study of a large series of Coot skeletons, that the variability of those proportions on which Böker chiefly relies (intramembral proportions) is usually less than 3% (standard deviation less than 3% of mean). Comparable results (Engels, 1940) were obtained in a previous study on thrashers (*Toxostoma*). In these statistical studies on proportions one encounters striking examples of individual constancy to type such as the following. In thirty-six specimens of Palmer's Curve-billed Thrasher (*Toxostoma curvirostre palmeri*), the humerus averaged but slightly *shorter* than the femur (98.8%) in length; in only four of the thirty-six individuals was the humerus longer than the femur (up to a maximum of 101.5% of femur). In twenty-one specimens of Bendire's Thrasher (*Toxostoma bendirei*) the humerus averaged only slightly *longer* than the femur (101.7%) and in none of the individuals was the humerus shorter than the femur. Here, then is a case of two related species—remarkably difficult to distinguish from each other in the field—in each of which the humerus and the femur are approximately equal in length, with a slight average difference favoring in one the humerus, in the other the femur; yet the overlap of individual variation is so slight that almost any pair of individuals

taken at random will exhibit the essential difference. These examples are of *inter*membral proportions, chosen because they happen conveniently to deal with bones of very nearly equal length; but it has been shown (Engels, 1938a) that correlation in length of parts is even closer *intra*membrally (e.g., within the wing) than it is intermembrally (i.e., between wing and leg).

These studies have led me to the very general and, I believe, reasonable conclusion that a few specimens, even single specimens, will suffice to reveal strongly contrasting patterns of proportion; but that large series of individuals and statistical treatment are necessary to demonstrate the reliability of slight differences. Thus, the patterns shown by Böker (1927) in his original presentation do depict, with sufficient reliability, the major differences in the wing-skeletal proportions of the five forms illustrating his five major flight types (*Perdix, Corvus, Apus, Megalornis* and *Diomedea*). Contrarily, no great reliance can be placed on his later figures (Böker, 1935), showing subtypes, transitional types, and modified types, where the differences between adjacent forms are very slight (unless one confine his attention to the general picture of change, ignoring the individual forms).

Now, as to the second question, whether differences in proportions have, primarily, a functional or a phylogenetic basis, it seems best to make our analyses in closely knit phylogenetic groups. I have already demonstrated (Engels, 1940), on a statistical basis, that the several species of *Toxostoma* exhibit varying patterns of proportion, and that the interspecific differences within this genus can be explained on a basis of functional correlation. Again (Engels, 1938b), I showed that differences in the patterns of proportion in the wing skeleton seen in three genera of cuculiform birds accompany functional differences. In each of these two instances, however, we are dealing not with differences in *mode* of flight so much as with progressive loss of flight ability or tendency to flight as a means of locomotion, that is, with a reduction or regressive evolutionary phenomenon. These previously determined correlations of structure and habit, then, had to do with loss of function, or diminished function, of the wing, rather than with changes of function in active modes of flight. Therefore it seems worth while to record the results of a similar study on some North American falconiforms—a natural group whose members sometimes display striking dissimilarities in flight habits. The data for this study were obtained from skeletons in the California Museum of Vertebrate Zoology with the kind permission of the Director, the late Dr. Joseph Grinnell.

The following skeletons were available. Cathartidae: *Coragyps atratus*, 1; *Cathartes aura*, 4. Accipitridae: Accipitrinae: *Astur atricapillus*, 1; *Accipiter velox*, 9; *A. cooperi*, 3; Buteoninae: *Buteo borealis*, 15; *B. regalis*, 2; *Parabuteo unicinctus*, 1; *Aquila chrysaëtos*, 4; *Haliaeetus leucocephalus*, 1; Circinae: *Circus hudsonius*, 8; Pandioninae: *Pandion haliaetus*, 3. Falconidae: Polyborinae: *Polyborus cheriway*, 2; Falconinae: *Falco mexicanus*, 2; *F. sparverius*, 4. In consideration of the foregoing discussion, and in view of the small number of available specimens of most forms, it must be emphasized that the data here illustrated are not sufficient to indicate truly the probable differences between similar forms (e.g., the two species of *Falco*); they are intended to show differences in the general pattern of proportions (e.g., as between the two species of *Falco* on the one hand, the two species of *Accipiter* on the other) and for this purpose the material is entirely adequate.

As in the author's previous studies, cited above, measurements were made with dial-type calipers and read to the nearest 0.1 mm. For the wing elements, the measurements were taken across the articulating surfaces; length of manus is the sum of three measurements: of the carpometacarpus and of each phalanx of the second (longest) digit. Trunk length was taken as a straight line between two parallel planes, one passing across the anterior face of the last cervical vertebra (last vertebra with a free rib) and the other passing through the posterior face of the last vertebra in the synsacrum; the vertebral column was held straight meanwhile by a stick passing through the neural canal.

Study of the accompanying histograms (Text-figs. 1, 2, 3) reveals the presence of several distinct types or patterns in the proportions of the wing skeletons. First, with respect to relative length of the wing as a whole, there are two groups; in the one, the wing is shorter, being less than three times the trunk length (average height of the three right-hand columns of any one histogram less than the height of the left-hand column; Text-fig. 1, Text-fig. 3 in part); in the other group are those birds in which the wing is longer, the total wing length being more than three times the trunk length (Text-fig. 2, Text-fig. 3 in part). Only one of the species here considered (*Polyborus*) falls approximately on that (arbitrary) dividing line.
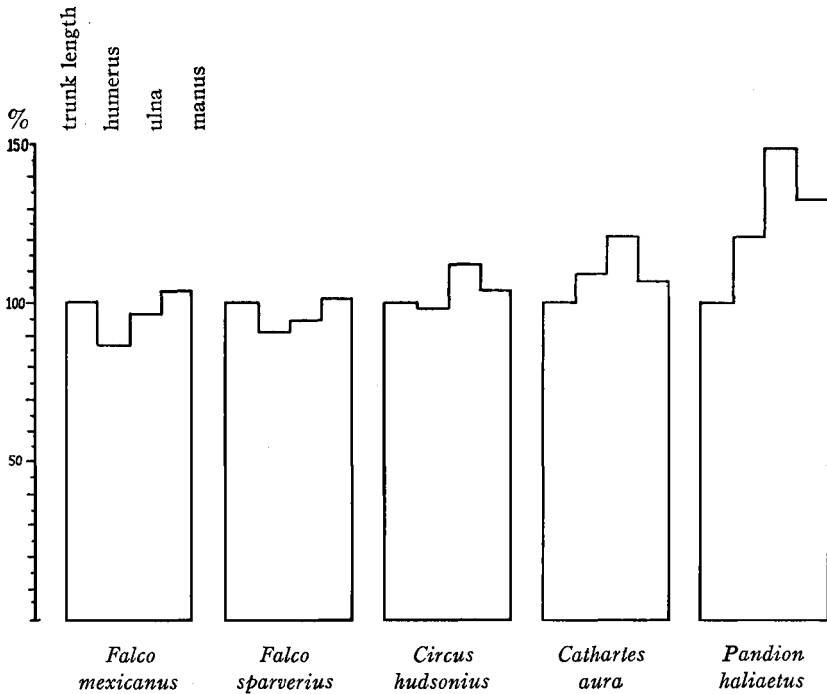
Next, with respect to the intramembral proportions (humerus: ulna: manus) it is apparent that two further groups are distinguishable, both in the short-winged and in the long-winged forms. Among the short-winged forms are some in which the ulna is the longest seg-
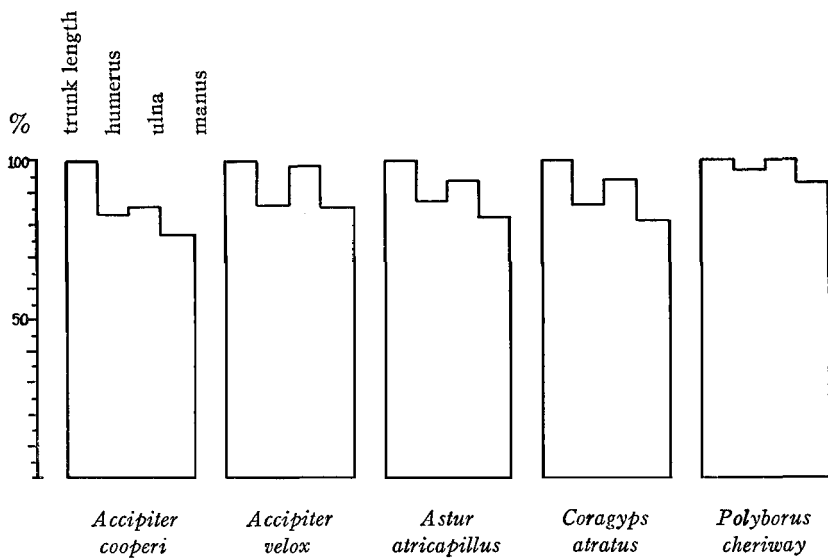
TEXT-FIG. 1.—Skeletal ratios in hawks.
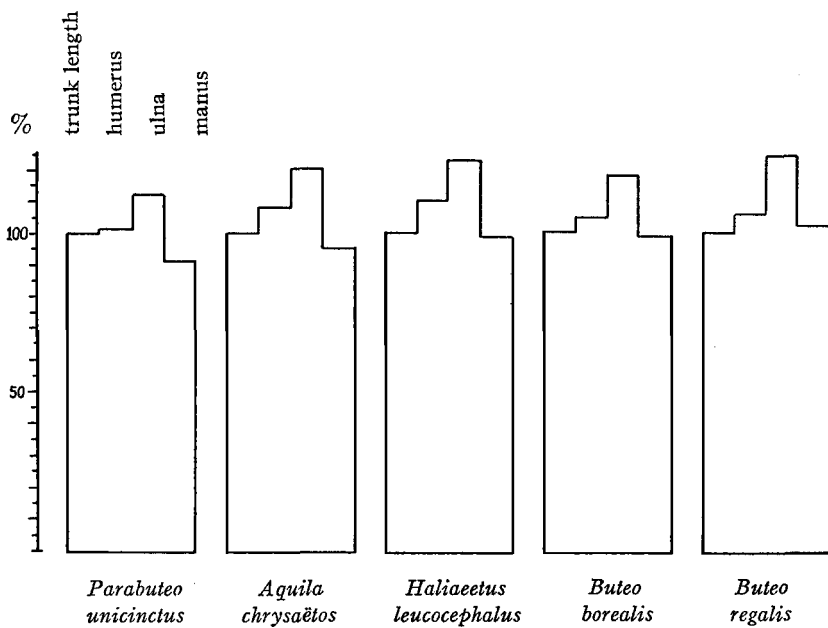
TEXT-FIG. 2.—Skeletal ratios in hawks.

TEXT-FIG. 3.—Skeletal ratios in hawks.

ment, the manus the shortest (Text-fig. 1: *Accipiter, Astur, Coragyps*); and others in which the manus is the longest segment (Text-fig. 3: *Falco*). Some of the long-winged forms are like the first-mentioned short-winged group, with shorter manus and longer ulna (Text-fig. 2: buteonines; Text-fig. 3: *Cathartes*); but others present a third pattern of intramembral proportions, in that the manus is intermediate in length between the longer ulna and the shorter humerus (Text-fig. 3: *Circus; Pandion*).

These patterns are summarized in the following scheme:

    A—short-winged
        a) manus < humerus < ulna
        b) humerus < ulna < manus

    B—long-winged
        a') manus < humerus < ulna
        c) humerus < manus < ulna

It is immediately striking that these several patterns are not distributed strictly in accordance with the accepted phylogenetic inter-

relationships of the forms here being considered. The falconid, *Poly-borus,* is not at all *Falco*-like, but is intermediate between two ac-cipitrid subfamilies, the buteonines and the accipitrines. One cathar-tid, *Coragyps,* resembles the accipitrines; while *Cathartes* is like the buteonines.

If we seek a functional basis for this morphogenetic similarity of phylogenetically dissimilar forms, some order appears, although there are manifest contradictions. The buteonines, which indulge in much soaring and circling on set wings and which otherwise appear some-what heavy and slow in their flapping flight, are all similar to one another in their wing proportions (Group $B — a'$ of the scheme above; Text-fig. 2). Some other soaring types fit into this scheme also, notably *Cathartes.* But while the intramembral proportions of still another soaring type, *Coragyps,* are similar, the whole wing is short, rather than long and therefore much like that of the accipitrines. This may be correlated, at least in part, with the very evident lesser soaring ability of *Coragyps,* as compared with *Cathartes;* but *Coragyps* must still be characterized as a soarer. The accipitrines are capable of soaring flight, but their short wings seem to be related to their more normal mode of flight, in which are stressed deep wing-strokes, and the dashing, twisting and turning in pursuit of prey in the bush.

It seems clear that the various proportion-patterns of the wing skeleton are at least as closely correlated with function as with family. But in some instances (here notably *Coragyps*) the functional correla-tion appears to be unsatisfactory. This is probably because numer-ous factors other than wing-skeletal proportions are operative in de-termining flight type. The wing skeleton and the proportions of its segments determine the basic leverage system of the wing, that is, they constitute the basic mechanical factors. In addition, two other sorts of factors, aërodynamic and psychobiological, are concerned; these depend indirectly on the mechanics of the wing skeleton.

One of the chief aërodynamic factors involved is the aspect ratio of the wing expanse, determined largely by the relative length of the flight feathers borne by the hand (primaries) and by the forearm (secondaries), but also determined in part by the length of the wing skeleton, both of the wing as a whole, and relative length of manus and ulna. The shape and position of the flight feathers (especially primaries) is also significant, whether broad and overlapping to their tips to form a completely air-resistant surface, or narrow and separated distally. Still other aërodynamic factors include the plane of the wing surface, the flight expanse and shape of the tail, the absolute

body size (weight) and the relative body size (relation to wing expanse).

The psychobiological factors are more subtle, but we cannot doubt their existence. The position of the wings in soaring, whether held in a horizontal plane (buteonines) or uptilted (*Cathartes*), may be of this sort, as well as the angulation of the wing (*Pandion*) and the spreading or folding of the tail-feathers in flight. Obviously psychobiological are the factors which determine preferential behavior in the air. Thus, the soaring sometimes indulged in by species of *Accipiter*, and said to be especially frequent in migration flights, indicates that they are fully capable of such flight, although their usual flight is of an entirely different nature. The courtship aëronautics of *Circus* may be contrasted similarly with its normal hunting flight.

Such factors are superimposed on the proportion-pattern of the wing skeleton and modify its functional significance. All factors, including skeletal proportions, represent the present stage in a continuous evolution. This introduces an historical (phylogenetic) factor. With respect to the skeletal proportions, the pattern seen in the accipitrines is probably near the generalized ancestral falconiform condition. Such generalized wing-skeleton proportions permit diversity of flight habit (in large birds); the type of flight actually performed depends in part on the psychobiological factors involved in preferential behavior, and, more especially, on modifications in the flight feathers (as well as absolute body size). These latter, aërodynamic, structural adaptations probably precede, in evolutionary time, those adaptive modifications of the skeleton involved in alteration of skeletal proportions. Thus, in *Coragyps*, the wing skeleton, although lengthened somewhat, retains the generalized intramembral proportions, but the flight feathers have been modified to give the broad wing characteristic of birds soaring on thermal air currents. The more thoroughly specialized soarers show not only the aërodynamic adaptations of great wing expanse (feathers!), but also a more greatly lengthened wing skeleton, with the hand especially increasing in relative length.

The falcons contrarily, in their swift, dashing flight, have retained a relatively short wing, but the hand is markedly lengthened. The long hand, together with long primary flight feathers and short secondaries, results in a narrow, pointed wing. It is to be noted that this pattern of proportion as exhibited by the falcons is that characterized by Böker as *Schwirrflug* (*Apus*, Boker, 1927; also *Chaetura*). The relatively very short humerus, the longer ulna, and the very long hand are strikingly reminiscent of the limb proportions in

cursorial unguligrade mammals (e. g., horse). In the latter, it is well understood that the long manus and pes are an adaptation to speed, making both for great length of stride and rapid recovery. The wing-skeletal proportions of *schwirrfliegende* birds might be subject to an analogous mechanical explanation, the clarification of which is but one of the many problems of dynamic anatomy presented by birds and awaiting study.

Circus and *Pandion* can also be derived from the accipitrine type; in these forms the whole wing has elongated, as in the soaring types, but the hand is longer. This may be a secondary condition, imposed upon a primary soaring adaptation.

The foregoing is merely a suggestion as to the possible evolution of the types. Evidence probably could be obtained by comparative ontogenetic studies (cf. Böker, 1927).

GENERAL CONCLUSIONS

The intramembral proportions of the wing skeleton are not an infallible index to flight habit, except perhaps where they indicate an extreme pattern. In any instance, however, the skeletal proportions have to be considered in connection with various aërodynamic factors (aspect ratio, wing expanse, tail expanse, character of flight feathers, absolute and relative body size, et al.) as well as with psychobiological factors, such as are involved in preferential behavior. All these factors (mechanical, aërodynamic and psychobiological) represent, in Recent forms, the present stage in a continuous evolution; this consideration introduces a phylogenetic factor in flight habit, which can be analyzed by comparative functional-anatomical methods (also, for the first two sorts of factors, by comparative ontogenetic studies).

This brief survey indicates that a promising field of investigation lies open here, for the student who has access to large series of specimens of skeletons and alcoholics as well as of the conventional study-skins.

LITERATURE CITED

BÖKER, H.
    1927. Die biologische Anatomie der Flugarten der Vögel und ihre Phylogenie. Journ. f. Ornith., 75: 304–371.
    1935. Einführung in die vergleichende biologische Anatomie der Wirbeltiere. I. Bd. Gustav Fischer, Jena.
ENGELS, W. L.
    1938a. Variability in bone length and limb proportions in the Coot (*Fulica americana*). Journ. Morph., 62: 599–607.
    1938b. Cursorial adaptations in birds. Limb proportions in the skeleton of *Geococcyx*. Journ. Morph., 63: 207–217.

1940. Structural adaptations in thrashers *(Mimidae:* genus *Toxostoma)* with comments on interspecific relationships. Univ. California Publ. Zool., 42: 341–400, 24 text-figs.

University of North Carolina
  Chapel Hill, North Carolina