A CONTRIBUTION TO THE MORPHOLOGY AND PHYLOGENY OF THE FALCONIFORMES

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ABSTRACT: Morphological studies of the falconiforms have suggested that the group is polyphyletic. The basic goal of the study is to detail the anatomical variation observed in the 300-odd species, with major emphasis on the skeletal system, and to search for the meaning of similarities as well as differences. Similarities are evaluated in terms of being parallelisms, convergences or evidence of close relationship. The question is continually asked, are differences significant in terms of demonstrating lack of relationships or do they merely represent gaps in continua. The traditional pattern of tabulated points of similarity or difference--most of which are arbitrary (and ignore instances of approach or overlap)--is avoided on the grounds that the real value of such information is in understanding how it is arrived at. The diversity of views relative to anatomical features is explored in an effort to clarify methodology; however, methodology, as such, is not discussed separately, it is revealed by the treatment of the materials. The account does not dictate conclusions--although the writer's interpretations are included--but does try to expose the known sides of each question. The conclusion reached is that the four groups of falconiforms should not be associated in a single order. The Cathartidae and the Falconidae are recognizably related to other orders of birds while the Accipitridae and Sagittariidae cannot be associated more closely with each other than to other orders.

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INTRODUCTION

The Problem

The order Falconiformes, as currently defined (Mayr and Amadon, 1951; Wetmore, 1960; Brown and Amadon, 1968) is made up of five families of living birds, plus two of fossils. The interrelationships of some of these have been suspect and some authors have gone so far as to state that the suborder Cathartae and the family Sagittariidae of the suborder Falcones should be separated as distinct orders. The apparent heterogeneity of this array seems particularly worthy of investigation and analysis. The approaches developed might prove useful in the evaluation of other families and orders of birds.

It is not to be concluded from the assumed heterogeneity that the objective of this study is to dismember the order and to scatter its parts in some novel way. Recourse to the lengthy lists of associations for each family and aberrant genus compiled by Fürbringer (1888, vol. 2) should convince one that this is hardly possible. It is true that the study was undertaken with certain preconceived notions as to the relationships of the various parts of this order, but each of these ideas and its alternative(s) has been weighed again and again.

The method of "phylogenetic study" has been discussed at length by Hennig (1966), but I cannot follow his recommendations. I have sought to identify those "apomorphous" features which would identify

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the various taxa but with no more success than other systematists. I have looked for transformation series, again without success (the usual reticular relationships were seen). I started with the theory that this order is polyphyletic and have attempted to indicate as succinctly as possible, by summaries or tables where appropriate, how this conclusion has been reached both by me and by others. It may be that Hennig's system will prove applicable in the long run but it will require at least another step beyond that which I have taken; again, it may remain only a theoretical possibility.

I have looked in vain for model situations in Hennig that I could follow with the materials at my disposal. (I have been comforted by Hennig's inability to define the class Mammalia, pp. 215-216, a situation not unlike the definition of the falconiform groups.) In lieu of such a "definitive" method of analysis, I have been satisfied to "advance" our conception of the "order" by way of the comparative approach far beyond (I hope) that of Sushkin or Pycraft--whose works have served as models. This is a descriptive study in which comparisons, tested and evaluated, are used to determine relationships, based on the belief, and contrary to Hennig, that this still is the only practical way.

The examples of paraphyletic (and polyphyletic) associations that sometimes result from such an approach are well known to evolutionary systematists as are the failures of "overall similarities" to reveal real relationships. Like others, although striving to identify monophyletic groups and abhoring paraphyletic or polyphyletic groups, I prefer a "typological" or syncretic system in which birds are identified as a class with an order, or orders, for the falconiforms. I have not dwelt here on methodology, as I feel that it is best revealed by the treatment of examples.

The goal of this study is to determine in detail the anatomical variation in each of the groups of falconiforms that have been recognized and to assess the differences and similarities in terms of phylogenetic relationship, or lack of it. This does not involve the compilation of tables of unanalysed anatomical details to be treated in some numerical fashion (Gadow, Fürbringer, and others). The study is, as far as possible, an original descriptive anatomy based on comparisons of homologous features and the evolutionary trends of such features; it involves recognition of nonhomologous, parallel or convergent features and their evaluation,so that they can participate in the establishment or disestablishment of groups.

A consideration of the anatomical facts, as described here, will lead directly to the conclusions--at least in terms of the hypotheses presented. These hypotheses relate to the identification of phylogenetically important features and the directions of change in each feature. Such hypotheses are more meaningful if the fossil record is extensive. In birds, such is not the case.

Without fossils, the selection of phylogenetically important features may be based on the palimpsest theory of Gregory (1947), which assumes that one can separate those anatomical details which have been modified in adaptation (habitus) from the underlying structural pattern (heritage) indicative of the ancestry of the species. The problem is not quite this simple, since Richardson (1942:234-236) pointed out that the new adaptive features are

superimposed on old. Thus, the heritage itself consists of successive layers of adaptive features.

It has been suggested that the discovery of useful anatomical features with which to characterize the diurnal predators is made difficult by the profound modifications needed for their raptorial existence. Such extreme adaptations, if shared as a common habitus, could prove either common ancestry or convergence. Since such a common habitus is not apparent, an alternate view would be that only limited modification was required to produce the several types of predators from distinct ancestral types (not sharing a common heritage).

Studies of parallel or convergent adaptations in other birds (Richardson, 1942; Stolpe, 1935) show that superficial agreement in way of life and method of locomotion (*Hesperornis*, loon, grebe; auk or heron, crane, stork, flamingo) may alter greatly the general proportions, but many minor details of structure reveal the heritage. If the falconiform groups are interrelated, then the problem is one of discovering underlying similarities, or combinations of basic features shared by the different families of this order. It is doubtful if the hooked bill and carnivorous habit originally used in the association of these families constitutes the heritage. If the falconiform groups are not interrelated, then comparisons with other kinds of birds may lead to identification of the heritage.

The determination of phylogenetically important features is not made easier by reports in the literature. First the American student is handicapped by the inaccessibility of major works written in foreign languages and of such mass as to defy adequate translation without mastery of these languages. Second, the foundation works belong to the last century and there has been continued development of the subject, or at least in the interpretation of its facts. Third, in the opinion of the writer, the jargon of anatomy makes understanding and comparisons difficult and at times impossible. Last, there has been far too much deference to authority (although authorities are frequently right) and far too little effort directed toward broad systematic investigations.

From the anatomical reviews in the literature, most features seem to fall into one of three categories: relatively uniform from species to species, variable without apparent phylogenetic or functional correlation, or adaptive. Any of these is of questionable value for establishing relationships, with the result that, having chosen from the available criteria, we seem to be torn between separating groups on the basis of certain characteristics and uniting them on others. Utilizing what appears to be the same "facts," two morphologists may come up with conflicting conclusions.

The difficulties of identifying and using phylogenetically important features will become increasingly evident in the following chapters. The greatest difficulty will be to overcome some of the prevalent views concerning avian anatomy and its taxonomic utilization. Unfortunately, the "facts" do not reveal a "black and white" situation, nor do they fix even the shades of gray. This indeterminacy of result is in itself important since it helps to destroy the belief which exists, in spite of much evidence to the contrary, that simple "key characters" can be defined and utilized,

at least in the case of the Falconiformes.

Finally, assuming that the anatomical facts can be marshaled to support a phylogeny, changes in existing classification may be necessary. Such changes are not always desired for reasons of "practicality" or common usage (*see* Sylvester-Bradley, 1956). The view is widespread that there should be no alterations in the present system (which system is not usually specified) until a completely satisfactory replacement is devised. A goal of this study is not to argue changes, *per se*, but to speed the time of an over-all revision based on thorough studies of many, if not all, orders of birds.

The approach

The systematic investigation, as it was finally conceived, began in 1945 while the author was at the University of California at Berkeley and was carried on thereafter at intervals through loans of material and visits to different places where the necessary specimens could be examined. After spending the summers of 1954 amd 1955 at the Museum of Comparative Zoology of Harvard, a final draft was completed in 1958. The present revision represents an attempt to bring the manuscript up to date in terms of the literature, but not to totally rethink it, nor to alter the original approach. Effort has been made to reword and shorten the text where this can be done without serious loss of information.

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Survey of the Literature

The number of titles related to the morphology and phylogeny of the falconiforms is large but the relevant content is limited. Alix (1874b), Fürbringer (1888), Gadow and Selenka (1891-93) and Sushkin (1905) present reviews which need not be duplicated; however, a few of the major contributions to our knowledge of the falconiforms, and particularly to the problem of phylogeny, should be cited.

Examples of studies of the morphology and phylogeny of orders of birds, which served as models, are Forbes (1882) on the procellariforms and Watson (1883) on the sphenisciforms. These accounts are too brief for extensive comparisons with other orders, but in spite

of this, they have added materially to our knowledge of bird anatomy.

Systematic studies of anatomy can be said to have begun with Nitzsch's (1840) "System der Pterylographie," but this is an arbitrary point, chosen for the methodology shown. The major contributors were Garrod (1873, 1874), Forbes (1884), Fürbringer (1888), Gadow and Selenka (1891, 1893) and Beddard (1898). More recent summaries are those of Stresemann (1927-34), Grassé (1950) and Sibley and Ahlquist (1972). Limited contributions are those of Chandler (1916), and Hudson (1937, 1948).

The anatomy of the falconiforms has not been neglected. Aldrovandi (1581-1603, 1610) described the muscles of the golden eagle, Merrem (1781) the bones and muscles of a hawk, possibly the honey buzzard. A. Milne-Edwards (1867-71) described and figured the osteology and myology of the golden and wedge-tailed eagles. A figure by Carus (*see* Coues, 1884, 1890, fig. 39) of the superficial myology of *Accipiter nisus* has been widely reproduced in different texts. Recent accounts include Compton's (1938) study of pterylosis of the falconiforms, Fisher's (1939 to 1947) descriptions of the cathartids and Berger's (1956b) account of the locomotor muscles of *Polihierax*.

Regarding the taxonomy of the falconiforms there have been the usual lumpers and splitters at work. Although the earliest authors united the owls with the diurnal birds of prey, some of the later ones have made the falconiforms a part of even more inclusive categories (Table 1). Huxley (1867) created orders

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Table 1. Samples of taxonomic systems in which the falconiforms are a part of more inclusive groups.

Huxley (1867
Order III. Carinatae
- Suborder 1. Dromaeognathae
- Suborder 2. Schizognathae
- Suborder 3. Desmognathae
  - Chenomorphae
  - Amphimorphae (Phoenicopteridae)
  - Pelargomorphae (Ciconiformes)
  - Dysporomorphae (Pelicaniformes)
  - Aetomorphae
    - Falconiformes
    - Strigiformes
  - Psittacomorphae
  - Coccygomorphae
  - Celeomorphae (Piciformes)

Garrod (1874)
Order III. Ciconiiformes
- Cohort a Pelargi (Ciconiidae)
- Cohort b Cathartidae
- Cohort c Herodiones (Ardeidae)
- Cohort d Steganopodes (Pelicaniformes)
- Cohort e Accipitres
  - Family 1 Falconidae
  - Family 2 Strigidae

Fürbringer (1888)
Order Pelargornithes
- Suborder Anseriformes
- Suborder Podicipitiformes
- Suborder Ciconiiformes
  - Gens Phoenicopteri
  - Gens Pelargo-Herodii
  - Gens Accipitres
    - Family Gypogeranidae

Oliver (1945)
Superorder Larimorpha
- Order Sphenisciformes
- Order Procellariiformes
- Order Colymbiformes
- Order Pelecaniformes
- Order Anatiformes
- Order Ardeiformes
- Order Podicipediformes

Family Cathartidae
Family Gypo-Falconidae
Gens Steganopodes

Order Gruiformes
Order Falliformes
Order Charadriiformes
Order Strigiformes
Order Accipitriformes

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according to the types of palate. Such a system received little support because of its many artificial associations. It did, however, focus upon an osteological area which, since that time, has engaged considerable attention. Garrod (1874) based his classification largely on myology and arrived at groups which resemble those set up somewhat later by Fürbringer (1888). Oliver (1945), using the form of the vomer as his main criterion, united the Accipitriformes with a great array of other birds in a superorder. Although these schemes are usually dismissed, they have virtue in that they point-up what is usually conceived of as an order is difficult to characterize anatomically and might better be considered a family--if it were not for the large number of species involved.

The general trend in systematics has been for the refinement of groups (Table 2). Brandt (1853) retained the owls with the

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Table 2. Subdivisions of the falconiforms in some different systems.

Lesson (1830-31)
- II. Oiseaux Normaux
  - Ordre Accipitres
    - Sect. I. Accipitres Gallinacees
      - Fam. 1. Serpentariees
    - Sect. II. Accipitres Diurnis
      - Fam. 1. Vautours
      - Fam. 2. Falconees
        - Les Ignobles
          - Tribe 1. Caracaras
          - Tribe 2. Aigles
          - Tribe 3. Autours
          - Tribe 4. Milans
          - Tribe 5. Buses
        - Les Nobles
          - Tribe 6. Faucons
    - Sect. III. Accipitres Nocturnes

Ridgway (1874)
- Order Falconiformes
  - Fam. 1. Cathartidae
  - Fam. 2. Gypogeranidae [Sagittariidae]
  - Fam. 3. Falconidae
    - Subfam. Falconinae
      - Group 1. Falcones
      - Group 2. Polybori
      - Group 3. Micrastureae
      - Group 4. Herpetotheraeae
    - Subfam. Buteoninae
      - Group 1. Pandiones
      - Group 2. Pernes
      - Group 3. Elani
      - Group 4. Ictiniae
      - Group 5. Circeae
      - Group 6. Nisi
      - Group 7. Geranospizae
      - Group 8. Urubitingae
      - Group 9. Buteones
      - Group 10. Haliaëti (Milvus)
      - Group 11. Aquilae
      - Group 12. Circaëti
      - Group 13. Archibuteones
      - Group 14. Vulturinae

Gadow (1893)
Order Falconiformes
  Suborder Cathartae
    Fam. Cathartidae
  Suborder Accipitres
    Fam. Gypogeranidae
    Fam. Vulturidae
    Fam. Falconidae
      Subfam. Gypaëtinae
      Subfam. Aquilinae
      Subfam. Buteoninae
      Subfam. Accipitrinae
      Subfam. Polyborinae
      Subfam. Falconinae
    Fam. Pandionidae

Sushkin (1905)
Order Falconiformes
  Suborder Cathartae
  Suborder "Serpentariae"
  Suborder Accipitres
    Fam. Falconidae
      Subfam. 1. Herpetotherinae
      Subfam. 2. Polyborinae
      Subfam. 3. Poliohieracinae
      Subfam. 4. Falconinae
    Fam. Aquilidae
      Subfam. 1. Pandioninae
      Subfam. 2. Perninae
      Subfam. 3. Milvinae
      Subfam. 4. Haliaeetinae
      Subfam. 5. Aquilinae
      Subfam. 6. Circaëtinae (Circinae)
      Subfam. 7. Vulturinae
      Subfam. 8. Urubitinginae
      Subfam. 9. Butasturinae
      Subfam. 10. Buteoninae
      Subfam. 11. Accipitrinae

Peters (1931)
Order Falconiformes
  Fam. Cathartidae
  Fam. Sagittariidae
  Fam. Accipitridae
    Subfam. 1. Elaninae
    Subfam. 2. Perninae
    Subfam. 3. Milvinae
    Subfam. 4. Accipitrinae
    Subfam. 5. Buteoninae
    Subfam. 6. Aegypiinae
    Subfam. 7. Circinae
    Subfam. 8. Circaetinae
    Subfam. 9. Pandioninae
  Family Falconidae
    Subfam. 1. Herpetotherinae
    Subfam. 2. Polyborinae
    Subfam. 3. Polihieracinae
    Subfam. 4. Falconinae

Wetmore (1951a, 1960)
Order Falconiformes
  Suborder Cathartae
    Superfamily Neocathartoidea
      Fam. Neocathartidae
    Superfamily Cathartoidea
      Fam. Cathartidae
      Fam. Teratornithidae
  Suborder Falcones
    Superfamily Sagittarioidea
      Fam. Sagittariidae
    Superfamily Falconoidea
      Fam. Accipitridae
      Fam. Pandionidae
      Fam. Falconidae

Brown and Amadon, 1968 (also Storer, 1971)
Order Falconiformes
  Suborder Cathartae - New World vultures
    Superfamily Neocathartoidea (fossil)
      Fam. Neocathartidae
    Superfamily Cathartoidea
      Fam. Cathartidae
      Fam. Teratornithidae (fossil)
  Suborder Accipitres
    Superfamily Accipitroidea
      Fam. Pandionidae - ospreys
      Fam. Accipitridae - kites, hawks, eagles, Old World vultures

Superfamily Sagittarioidea
Fam. Sagittariidae - secretary birds
Suborder Falcones
Fam. Falconidae - falcons, caracaras
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diurnal predators but differentiated the New and Old World vultures--as did Nitzsch (1840). Brandt, again following Nitzsch, was one of the first to give internal anatomy an important taxonomic role. The diagnoses are composed of external characters, including pterylography, and a scattering of osteological and myological facts; they have scarcely been improved on in more recent works.

Fitzinger (1856) separated the falconiforms and owls as distinct orders. Milne-Edwards (1867-71) and Fürbringer (1888) established the independent nature of the owls and placed them next to the Caprimulgiformes. Berlioz (Grassé, 1950) denied the caprimulgid affinity of the owls and returned them to a place next to the falconiforms. Engelmann (1928) also linked the diurnal and nocturnal birds of prey in the same order.

Following the splitting off of the owls, the Rapaces were further dismembered by Garrod (1874) and Forbes (1884) who separated the New World vultures (Cathartidae) and *Sagittarius*. Forbes allied the latter with the rails, bustards, and *Cariama*, while Garrod placed it with a combined gallinaceous-bustard group. Garrod (1874:114) commented that "The *Accipitres*, as generally defined, are not a natural group at all; and the *Cathartidae* are not the least more nearly related to the *Vulturidae* than to the Falconidae." Sharpe (1899) recognized three orders making up the Rapaces: Cathartiformes, Accipitriformes, and Strigiformes. He restored *Sagittarius* to the Accipitriformes.

The cathartids have been considered by most to represent primitive Falconiformes (Pycraft, 1902; Sushkin, 1905; Menzbier, 1916; Peters, 1931; etc.) although some recent writers (Chapman, 1926, and Griscom, 1932) have reasserted the independence of this group as a separate order without offering any supporting evidence. Hudson (1948) separated both the cathartids and *Sagittarius* as distinct orders on the basis of their hind limb myology. Ligon (1967) included the Vulturidae (Cathartidae) in a suborder Sarcorhamphi of the order Ciconiiformes.

The modern classification of the falconiformes began with Robert Ridgway (1874, 1875), who combined both external and internal characters. Ridgway was the first to demonstrate the osteological differences between the Falconidae and the Accipitridae and associated together for the first time such aberrant genera as *Polyborus*, *Micrastur*, and *Herpetotheres*. In spite of the magnitude of the demonstrated differences, he accorded the hawks and falcons only subfamily status.

Sushkin (1905) carried the contrasting of the Falconidae with the Accipitridae further and gave minute attention to the osteology of the Falconidae. His work represents a peak in the comparative study of a single family and has produced a clearer understanding of the order as a whole. He viewed the magnitude of differences between these families as greater than usual for

other birds but did not believe that they should be more widely separated. Of lesser value have been his opinions regarding the importance of various diagnostic characters.

In contrasting the arrangement of the various subfamilies of the Falconidae the conclusions of Sushkin (1905) generally have been utilized. In the Accipitridae the situation is quite different, and lack of agreement is more evident. Several genera have proved especially difficult to assign.

The "kites"* as a group have puzzled the taxonomist,with the result that they have been variously arranged (Shufeldt, 1891). Of all the genera, *Pandion* has been the most troublesome. Compton (1938) reviewed the literature pertinent to this form and described its pterylosis. He suggested that the osprey (*Pandion*) is related to the cathartids (also Fisher, 1955). Hudson (1948) described the myology of the leg, but as yet no complete anatomical investigation has been carried out to determine its relationships.

Sushkin (1899a, 1900) apparently attempted to solve the problems of interrelationships within the Accipitridae but such genera as *Geranospiza, Haliaeetus,* and *Terathopius* and the subfamily Aegypiinae cannot even now be satisfactorily associated with the more typical accipitrids.

The falconiforms are well represented in the fossil materials of birds. Important contributions have been made by the descriptions of many species by Loye Miller, Howard, and Wetmore. Particularly important for their lists of fossil species are the accounts of Lambrecht (1933), Wetmore (1940, 1956), Howard (1937-38, 1946) and Brodkorb (1963). Two new families, the Neocathartidae and Teratornithidae, allied with the Cathartidae in the suborder Cathartae, have been added to this order.

Fossil genera present several new problems that need thought, such as the species (or subspecies) in time and the degree, and kind, of similarity required for the taxonomic identification of a fragment. Simpson's (1946) study of penguins has indicated methods of treatment of fossil with modern species while LeGros Clark (1955) has emphasized the need for caution in describing and naming bone fragments which cannot properly be identified.

Materials and Their Analysis

Statements regarding specific details of methods and materials will be reserved for the chapters on each of the particular aspects of anatomy, but certain general remarks are in order here. A report of this type assumes that the reader has a rather detailed knowledge of the taxonomy of birds and particularly of the falconiforms. In reading about 300 species, 90 genera, several families and many subfamilies, the reader may be hard-pressed to keep everything straight. Also, many hawks do not have

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* *Elanus, Gampsonyx, Chelictinia, Machaerhamphus, Elanoïdes, Aviceda, Henicopernis, Pernis, Leptodon, Chondrohierax, Harpagus, Ictinia, Rostrhamus, Helicolestes, Milvus, Lophictinia, Hamirostra,* and *Haliastur. Gymnogenys* is usually associated with the harriers and is not included as a "kite" in most systems. *Pandion* is usually considered a "kite" and placed near *Pernis*.

generally accepted common names and are referred to by their generic name only (or occasionally by their complete scientific names--*see* Peters, 1931). It is hoped that by gradually developing the subject matter much of this confusion will be avoided. Therefore, this study is organized into several semi-independent sections or chapters starting with the exterior (ptilology), then the skeleton, myology, viscera, etc. Each section builds upon the conclusions of those preceding it.

A note on terminology is in order. The members of the family Falconidae will be referred to as falconids while the species of the subfamily Falconinae are collectively identified as falconins. These endings make possible the recognition of categories which are otherwise lost in such terms as falconine which includes both accipitrins and falconins. Also I have used the term falconiforms in place of the formal ordinal name of the diurnal birds of prey.

Anatomical terminology also needs a brief mention. I have used terms from a number of sources. The point here is not to discuss synonymys or argue homologies but rather to identify "bits" of information. Identification, in most cases, will be facilitated by the illustrations. Much of the detailed anatomy of birds is yet to be defined.

Since the initial goal of a balanced survey of all anatomical features could not be achieved due to lack of materials a fundamental linking anatomical system, the skeleton, was utilized. This was the only system for which adequate (but not complete!) materials were available. Other systems were investigated as thoroughly as possible. Specimens of twenty-six genera were totally dissected and individual species of several other orders were checked for specific points or to add general information on the variation between orders.

Because of the small number of preserved specimens which could be handled, a "selected representative species" approach was resorted to. In groups as large as two of the families of the falconiforms, it is not practical, or possible (specimens do not exist in collections) to dissect all of the species; rather one must determine those which probably are most aberrant by comparison of external and osteological features, or by reference to the literature, and dissect these in comparison with a "base" species representing one of the larger (having the most species) genera. Several of the most aberrant species were included in the dissection material, thus greatly increasing the range of known variation. As far as the falconiforms are concerned (with the exception of the cathartids which have been studied by Fisher), even a general picture of their anatomy is needed so as to make possible a more rapid advance towards a concise knowledge of their comparative anatomy.

The limitation of the number of specimens also raises the bogy of anatomical investigations; i.e., individual, sexual, and age variations (Berger, 1956a). Sexual variations in appearance are common in birds. In the falconiforms there is no apparent difference other than size, except in the cases of a few tropical eagles where the thickness of the legs differs markedly. Age variation generally is not involved since full growth is achieved shortly after leaving the nest. To determine individual

variation, several specimens of five species were dissected. Significant variation was not encountered--to the contrary, agreement within a species was exact,and closely related genera were so similar that external characteristics offered far better means of differentiating them. This does not mean that any single specimen is trustworthy; there is always the chance of encountering the exception, particularly in the large, specialized species (Fisher and Goodman, 1955). Frequently differences are unilateral so that comparison of both sides can be used as a check. The dissection of related species tends to point-up any extreme divergence in an individual. Although some abnormalities may have been observed without realization, the general uniformity of anatomy within assumed related groups suggested that this did not happen and that the variations observed were typical and reliable.

In analysis, more weight has been placed on the anatomical agreement among related forms than on minor details of differences. The differences that are most telling are those shared by all or most members of a group rather than those presented by a single specimen. In the cases of the monotypic *Sagittarius* and *Pandion* conclusions were based on several specimens. Three examples of the latter were dissected but only the pterylosis of two specimens of *Sagittarius* could be compared. However, on many of the questionable features, reports from the literature were used as confirmation. I feel that the materials sampled give a fair picture of the variation within the group, although contributions such as that of Berger (1956b) on the appendicular muscles of a pygmy falcon are always desirable.

In a study of comparative anatomy many decisions seem to be left to the bias of the writer. The various subjective evaluations that enter into a decision are functions of each problem. Therefore, one of my goals has been to present as much of the picture as possible. It is only by such a procedure that the reader can judge the value of any conclusions.

THE PTILOLOGY OF THE FALCONIFORMS

Definition and Procedure

Ptilology (May, 1945:1308) encompasses all aspects of feather study. Although having feathers is used as an identifying character of bird, there is much to learn about these epidermal structures: their evolutionary origin, development and variation of form, and adaptive modification. Pterylography, as the most discussed area, is still in an introductory state. The great need of ptilology is definition and a working hypothesis to explain the origin and the adaptive modification of the feather cover. This investigation has led to certain generalizations which answer this need. A detailed review of many aspects of ptilology has been done by Lucas and Stettenheim (1972).

Study of the ptilosis of birds began with Nitzsch (1840; English translation, Sclater, 1867), who described and figured the pterylosis of many birds. The distribution of the downs was described by Gadow and Selenka (1891). From time to time various papers have appeared describing the pterylosis of a single species or a small group; yet our knowledge of this field has scarcely

expanded.

The pterylosis of the falconiforms was studied by Compton (1938), who described three general types characteristic of three of the present families--Accipitridae, Falconidae, and Cathartidae. Miller and Fisher (1938) compared the pterylosis of the California condor (*Gymnogyps*) with that of the turkey vulture (*Cathartes*). Fisher, in a series of papers (especially 1943), presented descriptions of all the cathartids. Of the Accipitridae, *Milvus migrans* has been described by Al-Housaini (1938) and *Kaupifalco monogrammicus* by Verheyen (1953).

Verheyen's study included a discussion of some of the more general aspects of ptilosis. He points out that the feathers are arranged in rows (just as the scales of the fishes or reptiles--Breder, 1947) and that in the green pigeon, *Treron australis*, the number of rows (34-36) corresponds to the number of spinal nerves and sympathetic ganglia.

Another aspect of feather arrangement, which was studied by Goodchild (1886), is the lapping of the covert feathers on the wing. He defined several types, but the underlying reason (probably brought about by diastataxic shift) has not been discussed (Steiner, 1918).

The development of different types of feathers has been described (Strong, 1902, Lillie, 1942; Portmann, 1955), but the time of appearance and the detailed interrelationships of down and contour feathers has been generally ignored. The latter aspect was considered in a general way by Ingram (1920). *Gallus* and several charadriiforms were investigated in some detail by Gerber (1939). The latter's account shows that the regularly spaced contour feathers have down arranged amongst them and that each contour feather can be associated with one or more down feathers as a feather complex. This division of the plumage into a regularly spaced contour cover and an intermediate and somewhat irregular downy cover was remarked by Gadow and Selenka (1891:530). Studies similar to that of Gerber have been made by Maillard (1948), and Burckhardt (1954). Shelford (1900), Boulton (1927), Stewart (1952), Berger and Lunk (1954), and Wetherbee (1957) have described the pterylosis of nestlings.

The functional modifications of feathers on different parts of the body were investigated by Chandler (1914), who also reviewed and reported on their microscopic structure (1916). DeWitt Miller (1915; 1924a; 1924b) summarized such details of ptilosis as occurrence of eutaxy and diastataxy, presence of the aftershaft, and number of primaries or rectrices.

The subject of molting and the replacement of feathers has been summarized by Stresemann (1927-34), Stresemann and Stresemann (1960, 1966) and Grassé (1950). Jollie (1947) described the incomplete annual molt of the golden eagle, and Verheyen (1953:133) reported (probably in error) that *Buteo rufofuscus* and *Accipiter badius* in the Belgian Congo have two annual molts.

In studying the pterylosis of birds, Nitzsch (1867) employed three types of preparations: study skins, alcoholics, and fresh skins removed from the body to observe the bumps of the calami on the reverse side. A good proportion of his specimens was apparently examined as skins. Compton examined alcoholics and

his procedure for their preparation was followed by Fisher and myself. It involves clipping off the contour feathers near their bases and then plucking or clipping out the down to reveal the positions of the quills. In this study the distribution of downs has been noted along with that of the contour feathers.

Table 3 lists the study materials; it indicates by whom the

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Table 3. Materials examined in the study of pterylosis by Nitzsch (1840), Compton (1938), and the author.

	Nitzsch (1867)	Compton (1938)	Jollie	
Cathartidae				
Cathartes aura.	x	A	A 2	
Coragyps atratus.	x		A 1	
Sarcoramphus papa	x		A 2	
Gymnogyps californianus .	x		A 1	
Vultur gryphus.	x		A 2	
Sagittariidae				
Sagittarius serpentarius.	x	S	A 2	
Accipitridae				
Elanus caeruleus.	x		A 1	
Elanus leucurus		A	A 1	
Gampsonyx swainsoni . . .			A 2	
Elanoïdes forficatus. . .		S	S	
Aviceda cuculoïdes. . . .	x			
Aviceda subcristata . . .			A 1	
Pernis apivorus	x	S	S	
Leptodon palliatus. . . .			S	
Chondrohierax uncinatus .	x		A 1	
Harpagus bidentatus . . .	x		S	
Ictinia misisippiensis. .	x	A	A 1	
Rostrhamus sociabilis . .		S	S	
Helicolestes hamatus. . .	x		S	
Milvus milvus	x		A 1	
Haliastur indus		S	S	
Gymnogenys typicus. . . .		S	S	
Accipiter gentilis. . . .	x	A	A 3	
Accipiter cooperii. . . .		A	A 6	(3 nestl.)
Accipiter nisus	x		S	
Accipiter striatus. . . .		A	A 3	
Melierax metabates. . . .	x	S	S	
Buteo buteo	x		S	
Buteo jamaicensis		A	A 6	(3 nestl.)
Buteo harlani		A	A 1	
Buteo swainsoni		A	A 1	
Buteo lagopus		A	A 1	
Buteo regalis		A	A 1	
Kaupifalco monigrammicus.			A 1	
Leucopternis melanops . .	x		S	
Hypomorphnus urubitinga .	x		S	
Buteogallus anthracinus .	x		S	
Busarellus nigricollis. .	x		S	
Spizaëtus (tyrannus). . .	x		S	

	Nitzsch (1867)	Compton (1938)	Jollie
Hieraaëtus pennatus	x		S
Hieraaëtus fasciatus. . . .	x		S
Aquila chrysaëtos	x	A	A 5 (2 nestl.)
Uroaëtus audax.			A 2
Haliaeetus leucocephalus. .	x	S	A 2
Haliaeetus albicilla. . . .	x		S
Haliaeetus leucoryphus. . .	x		S
Haliaeetus vocifer.		S	S
Sarcogyps calvus.	x		S
Trigonoceps occipitalis . .	x		S
Aegypius monachus	x		S
Torgos tracheliotus	x		A 2
Gyps fulvus	x		S
Gyps ruppellii.			S
Pseudogyps africanus. . . .			S
Necrosyrtes monachus. . . .	x		A 1
Gypaëtus barbatus	x		S
Gypohierax angolensis . . .	x		S
Neophron perenopterus . . .	x		S
Terathopius ecaudatus . . .	x	S	S
Circaëtus gallicus.	x		S
Haematornis cheela.	x	S	S
Circus pygargus	x		S
Circus aeruginosus.	x		S
Circus cyaneus.	x	A	A 3
Pandion haliaetus	x	A	A 4 (1 nestl.)
Falconidae			
Herpetotheres cachinnans. .	x		A 1
Micrastur semitorquatus . .	x	S	S
Micrastur ruficollis. . . .			A 2
Daptrius ater	x		A 1
Milvago chimachima.	x		A 1
Phalcoboenus albogularis. .		S	S
Polyborus plancus		S	S
Polyborus cheriway.	x	S	A 2
Polihierax semitorquatus. .			A 1
Microhierax caerulescens. .	x		S
Falco rusticolus.	x	S	S
Falco mexicanus		A	A 2 (1 nestl.)
Falco peregrinus.	x	S	S
Falco aesalon	x		S
Falco subbuteo.	x		S
Falco tinnunculus	x		S
Falco sparverius.		A	A 3
Falco vespertinus	x		S
Falco concolor.	x		
Ieracidea berigora.			A 1

* *

specimens were examined, whether the specimen was an alcoholic (A) or a skin (S), and the number of specimens checked by the writer. The materials included some nestlings taken at, or before, the time of hatching.