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A Comparative Study of the Egg White
Proteins of Non-Passerine Birds

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ABSTRACT

The starch gel electrophoretic patterns of the egg white proteins of 816 species of non-passerine birds were studied. Evidence of family-level systematic relationships was sought and compared with published data on anatomy, behavior, hybridization, parasites, the fossil record, biochemistry, biogeography and egg shell structure. In many cases the previously accepted classification was supported; in others, questions were raised by the protein data. The history of avian classification is outlined, and the principal characters that have been used in the classification of birds are evaluated with the aid of published data.

It was concluded that: 1) the large ratites are monophyletic and evolved from a flying ancestor; 2) *Pelecanoides* is a procellariid; 3) *Cochlearius* is closest to *Nycticorax*; 4) the Phoenicopteridae are closer to the ciconiiforms than to the anseriforms, with a common ancestor for all three; 5) *Opisthocomus* is a cuculiform; 6) the Alcidae are closely related to the other charadriiforms; 7) *Tyto* is closely related to the Strigidae; 8) the Picidae and Capitonidae are closely allied.

It is probable that: 1) the nearest relatives of the Sphenisciformes are the Procellariiformes; 2) the Tinamiformes are closest to the Galliformes; 3) *Sula*, *Pelecanus*, *Phalacrocorax*, and *Anhinga* are closely allied; 4) *Scopus* is a ciconiid; 5) the New World Cathartidae are closer to the other diurnal raptors than to the Ciconiidae; 6) the Gruidae, Aramidae, Rallidae, Eurypygidae, Heliornithidae, and Turnicidae form a natural assemblage; 7) among caprimulgiforms two natural groups exist, one of the Aegothelidae and Podargidae, the other of the Caprimulgidae, Nyctibiidae, and Steatornithidae; 8) the Apodidae and Trochilidae are more closely allied than either is to any other group; 9) the Coraciiformes of Wetmore are polyphyletic; 10) the Alcedinidae and Todidae are closely allied.

Further conclusions on classification and relationships are given and ranked as possible or as improbable.

RÉSUMÉ

Les profils électrophorétiques sur gel d'amidon des protéines de blanc d'oeuf de 816 espèces de Non-Passereaux ont été étudiés. Des évidences des relations systématiques au niveau des familles ont été recherchées et ces résultats comparés aux données publiées concernant l'anatomie, le comportement, l'hybridation, les parasites, les fossiles, la biochimie, la biogéographie et la structure des coquilles d'oeufs. Dans de nombreux cas, la classification acceptée au préalable a été soutenue; mais dans les autres cas les données protéiques ont posé des questions. L'histoire de la classification des oiseaux est esquissée et la validité des principaux caractères utilisés pour la classification avienne a été évaluée à l'aide des données publiées.

Les suivantes conclusions sont considérées comme "très probables": 1) les grands Ratites sont monophylétiques et ont évolués à partir d'un ancêtre volant; 2) *Pelecanoides* est un procellariidé; 3) *Cochlearius* est l'oiseau le plus proche de *Nycticorax*; 4) les Phoenicoptéridés sont plus proches des Ciconiiformes que des Anseriformes, avec un ancêtre commun aux trois; 5) *Opisthocomus* est un cuculiforme; 6) les Alcidés sont de très proches parents des autres Charadriiformes; 7) *Tyto* est étroitement apparenté aux Strigidés; les Pucidés et les Capitonidés sont étroitement alliés.

Les relations suivantes sont "probables" : 1) les plus proches parents des Sphenisciformes sont les Procellariiformes; 2) les Galliformes sont les oiseaux les plus proches des Tinamiformes; 3) *Sula*, *Pelecanus*, *Phalacrocorax*, et *Anhinga* sont étroitement alliés; 4) *Scopus* est un ciconiidé; 5) les Cathartidés du Nouveau Monde sont plus proches des autres rapaces diurnes que des Ciconiidés; 6) les Gruidés, Aramidés, Eurypygidés, Heliornithidés et Turnicidés forment un assemblage naturel; 7) parmi les Caprimulgiformes deux groupes naturels sont distingués, les Aegothelidés et Podargidés d'une part, les Caprimulgidés, Nyctibiidés et Steatornithidés d'autre part; 8) les Apodidés et les Trochilidés sont plus proches entre eux qu'ils ne le sont séparément de n'importe quel autre groupe d'oiseaux; 9) les Coraciiformes définis par Wetmore sont polyphylétiques; 10) les Alcedinidés et les Todidés sont étroitement alliés.

D'autres conclusions sur la classification et sur des parentés sont mentionnées et désignées ou bien "possibles" ou bien "improbables".

ZUSAMMENFASSUNG

Die am Stärke-Gel durchgeforschten elektrophoretischen Muster der Eiweiss-Proteine von 816 Arten der Non-Passerés wurden untersucht. Beweise systematische Verwandtschaften auf dem Rang der Familien wurden gesucht und wurden mit ähnlichen veröffentlichten Beweise aus Anatomie, Verhaltens, Bastardierung, Parasiten, Paläontologie, Biochimie, Biogeographie, und Struktur der Eierschalen verglichen. In vielen Fällen wurden die angenommene Einteilung bestätigt; in anderen Fällen wurden Fragen von Seiten der Proteinangaben aufgeworfen. Die Geschichte der Einteilung der Vögel wurde skizziert, und die vorher in der Einteilung der Vögel benützte Hauptmerkmale wurden untersucht, mit Hilfe der veröffentlichten Data.

Zum Entschluss gekommen sind wir dass: 1) die grosse Flachbrustvögel sind monophyletisch; 2) *Pelecanoides* gehört zu den Procellariidae; 3) *Cochlearius* steht *Nycticorax* am nächsten; 4) die Phoenicopteridae stehen die Ciconiiformes näher als die Anseriformes, und alle Drei teilen einen Urahn; 5) *Opisthocomus* gehört zu den Cuculiformes; 6) die Alcidae sind nahe mit den anderen Charadriiformes verwandt; 7) *Tyto* und die Strigidae sind nahe miteinander verwandt; 8) die Picidae und die Capitonidae sind eng verbunden.

Aller Wahrscheinlichkeit nach: 1) die Procellariiformes sind die nächste Verwandten der Sphenisciformes; 2) die Tinamiformes stehen die Galliformes am nächsten; 3) *Sula*, *Pelecanus*, *Phalacrocorax*, und *Anhinga* sind eng verbunden; 4) *Scopus* ist ein der Ciconiidae; 5) die Neuweltgeier (Cathartidae) sind näher mit den anderen täglichen Greifvögel verwandt als mit der Ciconiidae; 6) die Gruidae, die Aramidae, die Rallidae, die Eurypygidae, die Heliornithidae und die Turnicidae bilden eine natürliche Versammlung; 7) die Caprimulgiformes bilden zwei natürliche Gruppen, die Eine der Aegothelidae und Podargidae, und die Andere der Caprimulgidae, Nyctibiidae und Steatornithidae; 8) die Apodidae und Trochilidae stehen einander näher als jede steht zu irgendeiner anderer Gruppe; 9) die Coraciiformes nach Wetmore sind polyphyletisch; 10) die Alcedinidae und die Todidae sind eng verbunden.

Weitere Entscheidungen über die Einteilung und die Verwandtschaften der Vögel werden beigebracht und in eine Reihe als "möglich" oder "unwahrscheinlich" gestellt.

Р Е З Ю М Е

Были изучены фигуры распределения протеинов белка 816 видов птиц из отряда не-воробьиных, полученные электрофорезом в крахмальном геле. Искались доказательства сродства между семействами; они тоже сравнивались с опубликованными данными анатомии, наблюдений над поведением птиц, гибридизации, с данными о паразитах, ископаемых, биохимии, биогеографии и о структуре скорлупы яиц. Во многих случаях раннее принятая классификация подтверждена; в других — данные изучения протеинов возбудили вопросы: Дается классификация пернатых, а главные характерные особенности, использованные для классификации птиц, оцениваются при помощи опубликованных данных.

Итак, были выведены заключения, что 1) большие нелетающие птицы являются монофилетическими и развились от летающих предков; 2) *Pelecanoides* это procellariid; 3) *Cochlearius* ближе всего к *Nycticorax*; 4) *Phoenicopteridae* ближе к формам ciconii, чем к формам anseri, с общим предком для всех трех форм; 5) *Opisthocomus* это форма cuculi; 6) *Alcidae* тесно родственны с другими формами charadrii; 7) *Tyto* близко родственна с *Strigidae*; 8) *Picidae* и *Capitonidae* являются тесно родственными.

Вероятнее всего, что 1) ближайшими родственными формами для *Sphenisci* являются формы *Procellarii*; 2) формы *Tinami* ближе всего к формам *Galli*; 3) *Sula*, *Pelecanus*, *Phalacrocorax* и *Anhinga* близко родственны; 4) *Scopus* это ciconiid; 5) *Cathartidae* Нового Света ближе к другим дневным хищникам, чем к *Ciconiidae*; 6) *Gruidae*, *Aramidae*, *Rallidae*, *Eurypygidae*, *Heliornithidae* и *Turnicidae* образуют натуральную группу; 7) среди форм caprimulgi имеются две естественные группы, одна состоящая из *Aegothelidae* и *Podargidae*, другая — из *Caprimulgidae*, *Nyctibiidae* и *Steatornithidae*; 8) *Apodidae* и *Trochilidae* гораздо ближе родственны друг к другу, чем каждая из них в отдельности к любой другой группе; 9) формы *Coracii* по Уйтмору (Wetmore) являются полифилетическими; 10) *Alcedinidae* и *Tolidae* являются близко родственными.

Дальнейшие выводы о классификации и родстве даются и классифицируются как возможные или как неправоподобные.

INTRODUCTION

The non-passerines are those birds not belonging to the order Passeriformes. This definition is convenient because it divides the class Aves approximately in half, with somewhat less than 4,000 of the 8,600 species of living birds being non-passerines.

The non-passerines represent the more ancient avian groups and include more aquatic forms. Although they are generally larger than passerines, among them are both the largest bird, the ostrich (*Struthio camelus*), and the smallest, the bee hummingbird (*Mellisuga helenae*). More non-passerines than passerines prey on vertebrates, and more are herbivorous, but few eat seeds.

Because of the structural diversity among non-passerines and the extinction of many intermediate groups, most non-passerine families and several of the orders are easily defined. The same factors, however, coupled with an inadequate fossil record, make it difficult to determine relationships among the higher categories. As yet, the degrees of relationship among the recognized orders are uncertain and the allocation of several families is a matter of debate.

Even within the past few years there have been major differences of opinion concerning the number of orders of non-passerines to be recognized. E. Stresemann (1959) divided them into 50 orders, but Wetmore (1960) used only 26. However, these classifications are basically nearly identical and the differences have occurred mainly because Wetmore accepted as orders the Gruiformes and Coraciiformes, each containing a heterogeneous assemblage of families most of which Stresemann treated as orders. Stresemann simply declined to unite families into orders where the evidence of relationships was not compelling.

Thus, although 99% of the species of birds have probably been described, there remain many questions concerning their classification into genera, families and orders.

The present study has two purposes. First, to review the literature of the classification of non-passerine birds, and second, to present new evidence of relationships from an electrophoretic study of the egg white proteins.

We have found it to be difficult to evaluate our new data without a critical and fairly detailed review of the previous evidence and opinions that support currently accepted classifications. We have therefore reviewed the literature pertaining to the higher category systematics of birds and we will present our reviews in three forms. The first is a brief chronological outline of the history of the classification of birds, the second is an evaluation of some of the principal characters used in avian classification, and the third is a review of the literature pertaining to each order. The first two reviews are presented in the introductory section which follows. The reviews of the literature concerning the orders are presented as part of the ordinal discussions. There is some repetition among these three reviews but we have tried to keep it to a minimum. We hope that by examining the subject from three viewpoints we have achieved a more balanced evaluation than that obtainable from a single method of organization.

A CHRONOLOGICAL SURVEY OF THE CLASSIFICATION OF BIRDS

While many systematists have regarded the Passeriformes as a morphologically uniform group and have despaired in their attempts to subdivide it, the relatively greater anatomical differences among non-passerines have provided the bases for a wide variety of opinions concerning relationships. The body of taxonomic literature concerning the non-passerines is therefore larger than for the passerines. In this brief review we have considered the work of those systematists who have treated the non-passerines more or less completely; the details of specific taxonomic proposals and their underlying rationale are covered in the accounts of each order. The emphasis is on the accounts of workers since the time of Darwin (i.e., 1859) but earlier authors who made a lasting impression on avian systematics have been included. Details, mainly of historical interest, on the work of these early ornithologists can be found in the introduction to Newton's *A Dictionary of Birds* (1893-96) and in E. Stresemann's *Die Entwicklung der Ornithologie* (1951).

Although the historical roots of ornithology can be found in the writings of Aristotle, Pliny, Turner and others (Newton, 1893-96: Introduction, 2-7) the earliest true classification of birds was produced by the collaboration of Francis Willughby (1635-1672) and John Ray (1628-1705). Newton (1893-96: Intro., 7) considered their work to be "the foundation of modern Ornithology" and Zimmer (1926: 677) called it "the cornerstone of modern systematic ornithology." The importance of the *Ornithologiae* (1676) of Willughby and Ray lies in its coverage of all birds known at the time and their arrangement into a logical, hierarchical classification. The main division was into "Land-fowl" and "Water-fowl," each of which was further subdivided upon the basis of other characters. An English translation was published in 1678.

The Willughby-Ray classification of birds was for the most part followed by Linnaeus (1707-1778) in his *Systema Naturae* and, according to Newton (1893-96: Intro., 8), "where he departed from his model he seldom improved upon it." Linnaeus provided a methodology for all systematic biologists and numerous classifications of birds based upon the Linnaean model were proposed during the century between the 10th edition of the *Systema Naturae* (1758) and Darwin's *Origin of Species* (1859).

The names of Edwards, Brisson, Buffon, Latham, Pennant, Cuvier, Illiger, Merrem, Vieillot, Lesson, Temminck, L'Herminier, Wagler, Gervais, Brandt, Bonaparte and others can be cited but their classifications were based mainly on external characters or relatively superficial comparisons of skeletal materials, and the differences between them are mainly those of arrangement.

The search for a theoretical framework for classification led a few ornithologists of the early 19th century to embrace the mystical nonsense of the "Quinarians," whose prophet was William S. MacLeay, an entomologist. Nicholas A. Vigors (1785-1840) and William Swainson (1789-1855) were the most prominent ornithologists who adopted and defended the Quinary System but this excursion into self-delusion was thoroughly discredited long before Darwinism provided a solid basis for systematics. Newton (1893-96: Intro., 31-35) has provided a review of the Quinarians and their negative impact upon the progress of avian systematics.

One of the first to investigate new characters for use in systematics was Christian Ludwig Nitzsch (1782-1837). Of a number of papers that he published, his studies on pterylography are the most significant. Nitzsch did not live to complete his *System*

der *Pterylographie* (1840) but it was edited and brought through press by C.C.L. Burmeister, who occasionally interjected his own interpretations of the pterylographic data.

The systematic works of George Robert Gray (1808–1872) strongly influenced 19th century ornithology, and some of his arrangements persist today. His *List of the Genera of Birds* was first published in 1840 and later followed by several editions. *The Genera of Birds* (1844–49) was an ambitious work of three folio volumes, and from 1869 to 1871 he published a three-volume *Hand-List of the Genera and Species of Birds*. Although Gray was not trained as a scientist, and his bases for classification were seldom more than external characters, his works had a lasting influence by providing a guide for arranging museum collections and organizing faunal surveys.

The pre-Darwinians lacked a unifying concept and depended mainly upon external characters. After 1858, evolution by natural selection provided the theoretical background for a rational search for evidence of common ancestries and the recognition of convergent evolution and its effects made superficial similarities unimportant unless supported by additional evidence.

Ornithologists were quick to embrace Darwinian concepts, perhaps because one of them, Thomas Henry Huxley (1825–1895) was also the most eloquent advocate of Darwin's ideas. Huxley's impact upon the classification of birds was enormous. As Gadow (1893: 33, transl.) noted: "The serious search for anatomical characters, as a basis for the natural system so often aspired to, began with Huxley." Huxley's famous paper on the avian palate (1867) provided the first of what was to be a series of attempts by his successors to find characters indicative of the relationships among the higher avian categories.

During the 30-year period from 1870 to 1900 the avian anatomists, primarily in England, Germany and the United States, were active and productive.

Carl Jacob Sundevall (1801–1875) was one of the first to use myological characters in avian taxonomy (1851). He questioned the idea, which apparently originated with Owen, that the ambiens functions to maintain a sleeping bird on its perch by producing a tension on the flexor muscles when the legs are folded. Sundevall also set off the Passeriformes (in which he included *Upupa*) because they lack a vinculum between the deep flexor tendons of the toes. It was not until many years later that the vinculum in the Eurylaimidae was discovered by Garrod (1877b).

In spite of his anatomical studies Sundevall's classification (1872–73) was based primarily upon external characters and was already an anachronism when published. He introduced a complex set of categorical names that was never adopted by others although his classification affected the arrangement proposed by Sclater (1880).

William Kitchen Parker (1823–1890) was primarily interested in the structure and development of the avian skeleton. Although he did not himself present complete classifications of birds his data were utilized by others and his papers included several that were explicitly oriented toward the systematics of the higher categories. Newton (1893–96: Intro., 79) credits Parker with breaking "entirely fresh ground" in his anatomical studies but Newton (p. 81) also criticized Parker for his frequent failure to interpret his observations in terms of systematic relationships. Parker's prose was often turgid and elaborate to the point of being unintelligible but his contributions are undeniable once the language has been understood.

The contributions of Alfred Newton (1829–1907) were less those of a participant than of an observant and often acerbic critic. His historical critiques (1884, 1893–96) provide a valuable review of the work of his contemporaries.

Alfred Henry Garrod (1846–1879) published his first ornithological paper in 1872 at the age of 26 and he died of tuberculosis when only 33 years old. During the intervening seven years, when he was Prosector of the Zoological Society of London, he

published 38 papers dealing with avian anatomy. His best known work was possibly that on the muscles of the thigh (1873d, 1874a) from which he derived the "pelvic muscle formula" that he and others have used to define and diagnose the orders and families of birds. Garrod also studied the nasal bones (1873a), the carotid arteries (1873b) and the deep plantar tendons (1875). In several papers he reported upon the tracheal and syringeal structure in various birds (see Forbes, 1881d).

Garrod's successor as Prosector of the Zoological Society was William Alexander Forbes (1855–1883), who died at 28 while on an expedition in Nigeria. Forbes was also prolific during his short life and produced a number of significant papers on avian anatomy and classification.

Philip Lutley Sclater (1829–1913) was the author of 582 papers on birds, many of which concerned the systematics of the non-passerines. He published a classification of birds in 1880 based upon the works of Huxley, Parker, Garrod and Sundevall, somewhat modified by his own work.

Leonhard Hess Stejneger (1851–1943), later to turn to herpetology, began his career in ornithology in 1882. His classification (1885) was favorably reviewed by Newton (1893–96: Intro., 98–100) and apparently had some effect on his successors.

Henry Seebohm (1832–1895) published a classification (1890a) that was dismissed as retrograde by Gadow (1893: 55). Newton (1893–96: Intro., 103), in one of his most sharply worded critiques, accused Seebohm of plagiarism and incompetence: "The author's natural inability to express himself with precision, or to appreciate the value of differences, is everywhere apparent, even when exercising his wonted receptivity of the work of others, and especially of Dr. Stejneger and Prof. Fürbringer." This harsh postmortem, written within a year of Seebohm's death, was tempered by the more charitable statement of Sclater (1896: 160), who described Seebohm as "kind-hearted and liberal, . . . and will be greatly missed by a large circle of friends."

Another prolific osteologist was Robert Wilson Shufeldt (1850–1934), who produced an astonishing array of descriptive papers between 1881 and 1923. Shufeldt often seems to have worked in a rather haphazard fashion, simply describing and comparing what he happened to have before him, but he placed on record an impressive number of observations over the more than forty-year span of his productive life.

Richard Bowdler Sharpe (1847–1909) was not a student of anatomy and he made few contributions to the classification of the higher categories. His classification (1891) was based upon the work of others and was the target of "much unfavorable criticism" (Allen, 1910: 128). Sharpe's great contribution was the 27 volumes of the *Catalogue of Birds in the British Museum* which were published between 1874 and 1898. Sharpe himself wrote eleven of the volumes and parts of three others. He edited or assisted with the remainder. The authors and volumes covering the non-passerines are as follows:

Sharpe: vol. 1, 1874, Falconiformes; vol. 2, 1875, Strigiformes; vol. 17, 1892, Leptosomatidae, Coraciidae, Meropidae, Alcedinidae, Momotidae, Todidae, Coliidae; vol. 23, 1894, Gruiformes in part; vol. 24, 1896, Charadriiformes: Charadrii; vol. 26, 1898, Ciconiiformes.

W. R. Ogilvie-Grant: vol. 17, 1892, Bucerotidae, Trogonidae; vol. 22, 1893, Galliformes; vol. 26, 1898, Pelecaniformes, Gaviiformes, Podicipediformes, Alcidae, and Sphenisciformes.

Osbert Salvin: vol. 16, 1892, Upupidae and Phoeniculidae; vol. 25, 1896, Charadriiformes: Lari, and Procellariiformes.

T. Salvadori: vol. 20, 1891, Psittaciformes; vol. 21, 1893, Columbiformes; vol. 27, 1895, Anseriformes, Tinamiformes, and ratites.

Howard Saunders: vol. 25, 1896, Gaviiformes.

Ernst Hartert: vol. 16, 1892, Apodiformes, Caprimulgiformes.

Edward Hargitt: vol. 18, 1890, Picidae.

P. L. Sclater: vol. 19, 1891, Ramphastidae, Galbulidae, Bucconidae.

G. E. Shelley: vol. 19, 1891, Indicatoridae, Capitonidae, Cuculidae, Musophagidae.

Peter Chalmers Mitchell (1864–1945) was the author of several works on avian anatomy that affected the classification of birds. He published on the condition of the fifth secondary (“quintocubitalism”), on the intestinal tract, the peroneal muscles and on the anatomy of several groups including the gruiforms and the kingfishers.

Maximilian Fürbringer (1846–1920) is primarily known to ornithologists as the author of two large volumes on avian anatomy and classification published in 1888. It is quite possible that Fürbringer’s work, in German and far too long for ready digestion, would have had little immediate effect upon English and American ornithologists had it not been for the existence of the ideal interpreter, the talented and bilingual Gadow. These two anatomists were to have the greatest impact upon avian classification during the next century.

Hans Friedrich Gadow (1855–1928) was born in Germany and studied anatomy under Haeckel and Gegenbaur. He began publishing in 1876 with a paper on the intestinal tract of birds, a subject which interested him throughout his life. Gadow went to England as a young man to work on the Catalogue of Birds, of which he compiled volumes 8 and 9. He became a British citizen, married the daughter of the Professor of Physics at Cambridge, and spent the rest of his life as Curator of the Stricklandian Collections and Lecturer, later Reader, on the morphology of vertebrates at Cambridge. He was the acknowledged authority on vertebrate anatomy in England.

Gadow admired Fürbringer but he was also critical of him. He noted (1892: 229) that Fürbringer’s “volumes of ponderous size have ushered in a new epoch in scientific ornithology. No praise can be high enough for this work, and no blame can be greater than that it is too long and far too cautiously expressed.” Gadow rejected Fürbringer’s intermediate categories but used his data, plus that from other sources, including his own research, to develop a new classification (1892, 1893). Based upon “about forty characters from various organic systems” (1892: 230) Gadow’s system became, and remains today, the basis for the accepted classifications of birds. Wetmore (1930: 1) recorded his debt to Gadow, and most of the other classifications published since 1930 have been based upon Wetmore and hence indirectly upon the Fürbringer-Gadow arrangement. For example, Peters (1931: v) cited Wetmore (1930) as the basis for the classification employed in his *Check-list of Birds of the World* and Mayr and Amadon (1951: 1) noted that they had departed from Wetmore’s arrangement only when changes were “clearly indicated by recent evidence.”

Gadow’s forty characters and the procedures he used to develop his classification are therefore highly pertinent to our discussion. Fortunately he was explicit on both points. The “List of the Characters employed in determination of the Affinities of the various Groups of Birds” is as follows (Gadow, 1892: 254–56):

A. Development.

Condition of young when hatched: whether nidifugous or nidicolous; whether naked or downy, or whether passing through a downy stage.

B. Integument.

Structure and distribution of the first downs, and where distributed.

Structure and distribution of the downs in the adult: whether absent, or present on pterylae or on apteria or on both.

Lateral cervical pterylosis: whether solid or with apteria.

Dorso-spinal pterylosis: whether solid or with apterium, and whether forked or not.

Ventral pterylosis: extent of the median apterium.

Aftershaft: whether present, rudimentary, or absent.

Number of primary remiges.

Cubital or secondary remiges: whether quinto- or aquinto-cubital.

Oil-gland: present or absent, nude or tufted.

Rhamphotheca: whether simple or compound, *i.e.*, consisting of more than two pieces on the upper bill.

C. Skeleton.

Palate: Schizo-desmognathous. Nares, whether pervious or impervious, *i.e.* with or without a complete solid naso-ethmoidal septum.

Basipterygoid processes: whether present, rudimentary, or absent; and their position.

Temporal fossa, whether deep or shallow.

Mandible: os angulare, whether truncated or produced; long and straight or recurved.

Number of cervical vertebrae.

Haemapophyses of cervical and of thoracic vertebrae: occurrence and shape.

Spina externa and spina interna sterni: occurrence, size, and shape.

Posterior margin of the sternum, shape of.

Position of the basal ends of the coracoids: whether separate, touching, or overlapping.

Procoracoid process: its size and the mode of its combination with acrocoracoid.

Furcula: shape; presence or absence of hypocleidium and of interclavicular process.

Groove on the humerus for the humero-coracoidal ligament: its occurrence and depth.

Humerus, with or without ectepicondylar process.

Tibia: with bony or only with ligamentous bridge, near its distal tibio-tarsal end, for the long extensor tendons of the toes; occurrence and position of an intercondylar tubercle, in vicinity of the bridge.

Hypotarsus: formation with reference to the tendons of the long toe-muscles:—(1) simple, if having only one broad groove; (2) complex, if grooved and perforated; (3) deeply grooved and to what extent, although not perforated.

Toes: number and position, and connexions.

D. Muscles.

Garrod's symbols of thigh muscles A B X Y,—used, however, in the negative sense.

Formation of the tendons of the m. flexor perforans digitorum: the number of modifications of which is 8 (I.-VIII.) according to the numbering in Bronn's *Vögel*, p. 195, and Fuerbringer, p. 1587.

E. Syrinx.

Tracheal, broncho-tracheal, or bronchial.

Number and mode of insertion of syringeal muscles.

F. Carotids.

If both right and left present, typical: or whether only left present, and the range of the modifications.

G. Digestive organs.

Convolutions of the intestinal canal. Eight types, numbered I.-VIII., according to Bronn's *Vögel*, p. 708, and P.Z.S. 1889, pp. 303-316.

Caeca: whether functional or not.

Tongue: its shape.

Food.—Two principal divisions, *i.e.* Phytophagous or Zoophagous, with occasional subdivisions such as Herbivorous, Frugivorous, Piscivorous, Insectivorous, etc.

List of Characters Employed occasionally.

Shape of bill.

Pattern of colour. Number of rectrices; and mode of overlapping of wing-coverts, according to Goodchild (P.Z.S. 1886, pp. 184-203).

Vomer. Pneumatic foramen of humerus.

Supraorbital glands.

Crop.

Penis.

Certain wing-muscles according to Fuerbringer.

Mode of life: Aquatic, Terrestrial, Aerial, Diurnal, Nocturnal, Rapacious, etc.

Mode of nesting: breeding in holes.

Structure of eggs.

Geographical distribution.

Gadow's procedure was a primitive type of numerical taxonomy but he did attempt to weigh his characters. He described his method as follows (p. 229):

The author of a new classification ought to state the reasons which have led him to the separation and grouping together of the birds known to him. This means not simply to enumerate the characters which he has employed, but also to say why and how he has used them. Of course there are characters and characters. Some are probably of little value, and others are equivalent to half a dozen of them. Some are sure to break down unexpectedly somewhere, others run through many families and even orders; but the former characters are not necessarily bad and the latter are not necessarily good. The objection has frequently been made that we have no criterion to determine the value of characters in any given group, and that therefore any classification based upon any number of characters however large (but always arbitrary, since composed of non-equivalent units) must necessarily be artificial and therefore be probably a failure. This is quite true if we take all these characters, treat them as all alike, and by a simple process of plus or minus, *i.e.* present or absent, large or small, 1, 2, 3, 4, &c., produce a "Key," but certainly not a natural classification.

To avoid this evil, we have to *sift* or *weigh* the same characters every time anew and in different ways, whenever we inquire into the degree of affinity between two or more species, genera, families, or larger groups of creatures.

This I have tried to do in a manner hitherto not applied to birds; it may have been done by others, but they have not published any account of this process. Certainly it has not been applied throughout the whole Class of Birds.

I have selected about forty characters from various organic systems (see Appendix, p. 254), preferring such characters which either can be expressed by a formula or by some other short symbol, or which, during the working out of the

anatomical portion of Bronn's 'Aves,' have revealed themselves as of taxonomic value, and of which I have learnt to understand the correlation, determining causes, and range of modification. Other characters, perhaps too complicated, too variable, or last, but not least, too imperfectly known in many birds, are left out or reserved for occasional employment.

Of my 40 characters about half occur also in Fuerbringer's table, which contains 51 characters. A number of skeletal characters I have adopted from Mr. Lydekker's [1891] 'Catalogue of Fossil Birds,' after having convinced myself, from a study of that excellent book, of their taxonomic value. Certain others referring to the formation of the rhamphotheca, the structure and distribution of the down in the young and in the adult, the syringeal muscles, the intestinal convolutions, and the nares, have not hitherto been employed in the Class of Birds.

Groups of birds, arranged in *bona fide* families, sometimes only genera of doubtful affinity, were compared with each other—each family with every other family or group—and the number of characters in which they agree was noted down in a tabular form. Presumably families which agree in all the 40 characters would be identical, but this has never happened. There are none which differ in less than about 6, and none which agree in less than 10 points. The latter may be due to their all being birds. It is not easy to imagine two birds which would differ in all the 40 characters.

In another table all the families were arranged in lines according to their numerical coincidences, and attempts were made to arrange and to combine these lines of supposed affinities in tree-like branches. These attempts are often successful, often disappointing. Of course this merely mathematical principle is scientifically faulty, because the characters are decidedly not all equivalent. It may happen that a great numerical agreement between two families rests upon unimportant characters only, and a small number of coincidences may be due to fundamentally valuable structures, and in either case the true affinities would be obscured. This it was necessary to inquire into. But at any rate I obtained many hints from this simple mode of calculation, indicating the direction which further inquiry should take.

The Psittaci may serve as an example of my mode of sifting characters.

According to the numerical agreement of the 40 characters employed generally, we have the following table:—

Psittaci agree with Cocyges in 31 points, with Pici in about 29, with Coraciidae 25, Falconidae 25, Striges 22, Bucerotidae 22, Gallidae 21, against 19 points of difference.

A previous line of investigation had revealed the fact that the Cocyges and Gallidae are intimately connected with each other through *Opisthocomus*. This knowledge obviated further inquiry as to the affinity between Psittaci and Gallidae.

Gadow presented the complete data for his comparisons between the parrots and other groups as an example of his method. He then presented his classification in which the characters of each group were listed under the name of the taxon. The result is impressive and it conveys a sense of careful and extensive comparisons based upon a large amount of work. Nothing as authoritative and complete had come before and subsequent workers could do no better than to base their classifications upon that of Gadow and, unless the evidence to the contrary was overwhelming, his conclusions were accepted.

The apparent success that Gadow had achieved may have been an important factor in the decline in interest in avian anatomy and higher category systematics that characterized the next half century or more.

That the Fürbringer-Gadow volumes had such an effect is indicated by the author's comment in the preface of his book *The Structure and Classification of Birds* (1898a) by Frank Evers Beddard (1858-1925): "It must be admitted that a handbook upon bird anatomy was more wanted at the time that it was first conceived by Mr. Garrod than it is at the present. . . . We now have two treatises of first-rate merit, that of Fürbringer and Dr. Gadow's completion of the section 'Aves' in Bronn's 'Thierreich'."

Beddard's own contributions began in 1884, when he succeeded Forbes as Prosector of the Zoological Society of London and continued until 1914. Although his volume was overshadowed by those of Fürbringer and Gadow it did provide a summary for English-speaking anatomists and is still a useful reference.

William Plane Pycraft (1868-1942) published a number of papers on avian morphology between 1890 and 1927. They included several on pterylography and osteology but most of his work was in relation to classification. From 1898 until 1933 Pycraft was in charge of the spirit and osteological collections of birds in the British Museum of Natural History.

Hubert Lyman Clark (1870-1947) wrote a series of papers on avian anatomy, especially on pterylosis, and published a classification of birds (1901b) which was based mainly upon pterylosis. Some of his proposed groupings make sense but several cannot be supported by other evidence. For example, Clark placed the procellariiforms with the ducks, pelicans and auks, and considered the penguins to be unique and separate. *Opisthocomus* he thought to be falconiform and the bustards were placed near the herons and storks. It is hardly surprising that this attempt was ignored.

Another attempt to use plumage characters was that of Asa Crawford Chandler (1891-1958), who published a study of the taxonomic significance of feather structure in 1916. He examined feathers microscopically and made a number of interesting taxonomic proposals, many of which do not seem to be valid.

Waldron DeWitt Miller (1879-1929) began his work on higher category systematics with a revision of the kingfishers (1912) and gave particular attention during the next 14 years to pterylosis and foot structure.

Percy Roycroft Lowe (1870-1948) began to publish papers on avian systematics in 1912 and was especially active during his tenure in charge of the Bird Room of the British Museum of Natural History from 1919 to 1935. Lowe's systematic works included anatomical studies of the shorebirds as well as important and sometimes controversial papers on the ratites, penguins, Galliformes, Coraciiformes and Piciformes.

Erwin Stresemann (1889-) began his long and brilliant career early in this century and succeeded Anton Reichenow as head of the Bird Department in the Berlin (Humboldt) Museum in 1921. Stresemann's numerous publications are principally systematic although most do not concern higher category relationships. However, his many papers on molt patterns, culminating in the publication of *Die Mauser der Vögel* (1966), co-authored with his wife, Vesta, is an important contribution.

The classification followed by Stresemann in writing the "Aves" section of Kükenthal and Krumbach's *Handbuch der Zoologie* (1927-34) was based primarily upon that of Fürbringer, somewhat modified by that of Gadow, but Stresemann declined to unite into a single order those groups which Gadow (1892) included in his Gruiformes. Similarly, Stresemann gave ordinal status to most of the subgroups in Gadow's Coraciiformes. Gadow recognized 20 orders but Stresemann divided the Aves into 49.

In 1930 (Frank) Alexander Wetmore (1886-) published the first of several

“editions” (1934, 1940, 1951, 1960) of his classification of birds. It was based upon Gadow’s (1893) arrangement, and Wetmore (1930: 1) acknowledged his debt as follows: “The work of Hans Gadow has been taken as a starting point, and such changes have been incorporated as seem justified from personal research or from the investigations of others. In general, only such variations from the current order have been accepted as seem to be firmly established. Where doubt tends to attach to any proposition, the older classification has been followed; so the following scheme presents a conservative arrangement so far as possible.”

In the later versions of his classification Wetmore has introduced certain modifications but the basic arrangement in the 1960 paper is still similar to that of Gadow (1893). The differences are mainly in the categorical levels assigned to various groups.

The Gadow–Wetmore classification has now been almost universally adopted and departures from it are viewed with skepticism. One notably unsuccessful attempt to promote a different classification was that of René Verheyen (1907–1961) who wrote a long series of papers between 1953 and 1961 in which he proposed radical new arrangements. Verheyen’s method was to make a large number of measurements of osteological characters and to subject the data to a crude kind of numerical analysis. In some cases he split up morphologically uniform groups into many monotypic genera, and in others he proposed alliances between taxa that for years had been acknowledged to be only convergently similar. Although Verheyen’s studies stirred controversy, his proposals were not accepted because he was unable to prove the relationships he suggested among the higher categories and, in most cases, there exists evidence contrary to his claims.

E. Stresemann (1959) castigated Verheyen and was pessimistic in his outlook for improvements in the systematics of higher categories: “As far as the problem of relationship of the orders of birds is concerned, so many distinguished investigators have labored in this field in vain, that little hope is left for spectacular breakthroughs. . . . Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after nearly 200 years of efforts. The rest is silence” (p. 277–78).

SUMMARY

The classifications of birds in use today are based upon that of Gadow (1892, 1893) which in turn was based primarily upon the data assembled by Fürbringer (1888). Huxley (1867), Garrod, Forbes and a few others also had some effect upon Gadow’s classification. Although there have been some changes in the sequence of the major groups and in the number of orders recognized, the classifications of Wetmore (1960) and of Gadow (1893) are virtually identical. Since Gadow (1892, 1893) provided a list of the characters upon which he founded his groups it becomes important to assess the taxonomic value of those characters. In the following section we have assembled data pertinent to such an evaluation of six of Gadow’s characters.

SOME OF THE PRINCIPAL CHARACTERS USED IN THE CLASSIFICATION OF BIRDS

It is not practical to undertake an analysis of all of Gadow’s forty characters so we have chosen six that represent a variety of anatomical systems, namely, palatal struc-

ture, pelvic musculature, deep plantar tendons, intestinal convolutions, carotid arteries and the fifth secondary. Any other selection would serve as well to illustrate our belief that all gross anatomical characters are subject to convergence but that all are also capable of providing insight into relationships at some taxonomic level. The problems arise when a character that is truly informative at one level is used to "prove" a taxonomic opinion at another.

Proposed changes in classification have little prospect of acceptance at the present time unless accompanied by overwhelming evidence that they represent a closer approach to a "natural" classification. To provide the sense of confidence that is required to surmount the hurdles of tradition and usage it is necessary to present new, convincing data and also to show that the evidence used by Gadow was not beyond question.

In the following section we will review six of Gadow's characters and present the discoveries which later workers have made concerning them.

1. PALATAL STRUCTURE

Although Cornay (1847) had proposed a classification based upon the palatal bones (see Newton, 1893-96: Intro. p. 69-70), it was Huxley (1867) who convinced ornithologists of their utility for classifying the higher categories. Huxley proposed four palatal types:

1) Dromaeognathous. Vomer broad posteriorly, interposed to prevent articulation of the basisphenoidal rostrum with pterygoids and palatines. The term "palaeognathous" is a synonym of dromaeognathous.

2) Desmognathous. Vomer small or absent; maxillopalatines meet in mid-line; pterygoids and palatines articulate with basisphenoidal rostrum.

3) Schizognathous. Vomer sometimes small, but present, usually terminating in a point anteriorly; maxillopalatines variable in size and shape, do not meet in mid-line with each other or with the vomer.

4) Aegithognathous. Vomer broad and truncate anteriorly; maxillopalatines do not join but do touch the basisphenoidal rostrum.

A fifth palatal type was suggested by Parker (1875b) for some Piciformes. This "saurognathous" palate has small maxillopalatines, hardly extending inward from the maxillae. Hence the skull is widely schizognathous.

The palatal types became the basis for major groupings of birds, "suborders" as Huxley called them. Within these groups Huxley arranged the families on finer distinctions of palatal morphology and other characters of the skull.

Newton (1868) moved quickly to counterattack with a critique that is a model of damning with *great* praise. He pointed out exceptions to Huxley's groupings and objected to the "single character" nature of Huxley's classification. Huxley (1868a) ably defended himself by showing that he did use other than palatal characters and that single characters were often excellent guides to affinity. This skirmish ended in a draw but it was only the first battle in a long war.

Some years later Newton (1893-96: Intro. p. 82-85) again reviewed Huxley's paper on the palate and again expressed his admiration for the author, but he attributed (p. 84-85) the acceptance of Huxley's proposals as much to the salesmanship of the author as to the power of his scientific discoveries:

That the palatal structure must be taken into consideration by taxonomers as affording hints of some utility there could no longer be a doubt; but the present writer is inclined to think that the characters drawn thence owe more of their

worth to the extraordinary perspicuity with which they were presented by Huxley than to their own intrinsic value, and that if the same power had been employed to elucidate in the same way other parts of the skeleton—say the bones of the sternal apparatus or even of the pelvic girdle—either set could have been made to appear quite as instructive and perhaps more so. Adventitious value would therefore seem to have been acquired by the bones of the palate through the fact that so great a master of the art of exposition selected them as fitting examples upon which to exercise his skill.

Beddard (1898a) reviewed the work of Huxley and Parker (1875a,b) on the palate and added numerous observations from his own studies. It was apparent to him that the desmognathous, schizognathous and aegithognathous palate types intergrade into one another, and that “neither are any of the subdivisions . . . really satisfactory from the classificatory point of view” (p. 140). Beddard found so many exceptions and intermediate conditions in palatal structure that he concluded (p. 150): “It appears, therefore, undesirable to lay too much stress upon the modifications of the palate . . . as a basis of classification.”

Pycraft (1900) proposed that the palate, rather than the sternum, should be the basis for the major subdivisions of birds. Under this arrangement the tinamous would be associated with the ratites as the Palaeognathae, the remaining carinate groups to be the Neognathae.

Pycraft (1901: 354) concluded that “the differences between the Palaeo- and Neognathine palate are those of degree and not of kind.” His discussion and conclusions seem to add little to the general debate but they further emphasize the lack of sharply definable palatal types and the existence of many intermediate conditions—in short, evidence that the palate, like all other structures, is adapted to the requirements of life in each case.

DeBeer (1937) pointed out that the “saurognathous” condition is not distinguishable from the “schizognathous” and that some “neognathous” forms are “palaeognathous” during embryonic development. MacDowell (1948) concluded that the palaeognathous and neognathous palatal types are not distinctive, cannot be defined morphologically and are actually composed of a heterogeneous assemblage of four distinct morphological conditions.

However, both Hofer (1945, 1955) and Simonetta (1960) considered the palaeognathous palate to be morphologically uniform although they were cautious about its taxonomic implications.

Bellairs and Jenkin (1960) reviewed the literature and pointed out the exceptions and the lack of sharp demarcations between the named palatal conditions and Bellairs (1964) concluded that (p. 592) “while palatal characters may be of value as a guide to the systematics of the smaller groups, they do not in themselves provide a reliable basis for major classification.”

The most recent analysis is that of W. Bock (1963), who restudied the skulls of the ratites (including the tinamous and kiwis) and redefined the palaeognathous palate. He contended that this palatal type is real but that the definition is not simple, rather that it depends upon a complex configuration of several features, as follows (p. 50):

- (a) The vomer is relatively large, and articulates with the premaxillae and maxillo-palatines anteriorly and (except for the ostrich) with the pterygoids posteriorly;
- (b) the pterygoid prevents the palatine from articulating with the basisphenoid rostrum;
- (c) the palatine articulates with the pterygoid along a suture;
- (d) the basitemporal articulation is large, and is found near the posterior

end of the pterygoid; (e) the articulation between the pterygoid and the quadrate is complex, and includes part of the orbital process of the quadrate; and (f) the palaeognathous palate as a whole presents a general configuration similar in all birds possessing it, and sharply distinct from the condition found in all other birds.

Bock used this evidence to support his argument that the ratites, including the tinamous and kiwis, are monophyletic. Bock's argument is partly circular and the validity of the palatal evidence actually depends upon independent proof that the tinamous and kiwis are closely related to the large ratites. Since we doubt that they are, we also doubt the value of the palaeognathous palate as an indicator of relationships. (See Sibley and Frelin, in press.)

2. PELVIC MUSCULATURE

Garrod (1873d, 1874a) proposed a classification based in part upon the presence or absence of certain muscles of the thigh region. In Garrod's scheme four muscles were designated by letter symbols and a "pelvic muscle formula" could then be written to designate the presence or absence of these four muscles in any group of birds. The four muscles, their code letter symbols and their modern synonyms (J. George and Berger, 1966: 233) are as follows:

GARROD'S NAME	MODERN SYNONYMS
A Femoro-caudal	Piriformis pars caudofemoralis
B Accessory femoro-caudal	Piriformis pars iliofemoralis
X Semitendinosus	Flexor cruris lateralis
Y Accessory semitendinosus	

In addition, the presence or absence of the ambiens was indicated by plus or minus signs. Thus a bird with all five of these muscles would be designated ABXY+ (or ABXY Am).

Garrod based his major subdivision of the Class upon the presence or absence of the ambiens. Those birds possessing it were designated "homalognatous," those lacking the ambiens "anomalognatous," and the two subclasses in his classification became the Homalognatae and the Anomalognatae. Garrod did not rely solely upon the ambiens, however, for he believed that other characters of pterylography, myology, oil-gland feathering and caecal development were correlated with the ambiens.

At first glance the correlations seemed quite convincing (Forbes, 1881d) but there were exceptions that had to be explained away. In some cases this led to associations that were disputed by other evidence. For example, the owls and goatsuckers lack the ambiens (= anomalognatous) but have the dorsal pterylosis pattern of the Homalognatae. Additional difficulties were pointed out by Newton (1893-96: Intro. p. 92-93), who concluded that "common sense revolts at the acceptance of any scheme which involves so many manifest incongruities."

Beddard (1898a: 95-97) showed that the ambiens is present in some storks, absent in others and absent from the herons but he noted the degrees of development of the ambiens in several groups and concluded that Garrod's two divisions based upon the ambiens could be supported. Most of Beddard's argument rested upon the work of Mitchell (1894), who described the relationships between the ambiens and the flexors of the leg. In some otherwise homalognatous birds (e.g., *Nycticorax*) which lack an obvious ambiens Mitchell found what he considered to be the rudiment of the ambiens, while in the unquestionably anomalognatous *Corvus* no such rudiment could be located.

Gadow (1892, 1893) used Garrod's formula but it is clear from his discussions (1891: 208; 1893: 37) that he considered the formula to be of limited value. In his list of characters (1892: 255) Gadow included Garrod's pelvic muscle symbols but noted that they were "used, however, in the negative sense." By this he seems to have meant that he used the muscle formula to distinguish between groups, as in the Steganopodes (= Pelecaniformes), rather than to indicate relationships.

Hudson (1937: 59-63) proposed that Garrod's formula be expanded by the addition of two muscles and a vinculum, as follows:

CODE LETTER	ITEM
C	M. ilio-trochantericus medius
D	M. glutaesus medius et minimus
V	Vinculum connecting the tendon of the flexor perforatus digiti III with that of the flexor perforans et perforatus digiti III

Hudson (p. 62) noted that in spite of the problems associated with using the myological formulae to indicate relationships they "can at least serve as aids in characterizing the higher groups of birds."

Hudson considered the muscle formulae to be of limited value but noted that an examination of the entire pelvic musculature could be informative. For example, the Fregatidae and Falconiformes have identical formulae using Hudson's expanded version of Garrod's formula but these two groups show "radical disagreement" when the entire musculature of the pelvic limb was considered. On the other hand, the similar formulae of the Piciformes and Passeriformes are supported by the similarity in all the other pelvic muscles as well.

Berger (1959) proposed the addition of three more muscles to the Garrod-Hudson set of eight items. These were as follows:

CODE LETTER	MUSCLE
E	Iliacus
F	Plantaris
G	Popliteus

J. George and Berger (1966: 233) reviewed the history of the pelvic muscle formulae and presented a table (p. 234-36) giving the formulae of groups for which it is known. They concluded (p. 236):

It is obvious that a leg-muscle formula tells nothing about the relative development or peculiarities of structure of the muscles, nor does it reveal anything about the approximately 36 other muscles of the pelvic limb. For understanding functional anatomy as well as phylogenetic relations, a knowledge of the complete myology is essential (see the discussion in Newton and Gadow, 1893: pp. 603-604). It is obvious, as well, that myological data must be used in conjunction with other information, both anatomical and biological, in order to ascertain phylogenetic relationships. Muscle formulas may yet prove useful in technical diagnoses of families or other taxonomic categories, but how useful remains to be determined.

3. THE DEEP PLANTAR (OR DEEP FLEXOR) TENDONS

Sundevall (1835) was the first to utilize "the properties of the hind toe and of the wing-coverts, which are characteristic of the true Passeres" (1872-73; transl. Nichol-

son, 1889: 4). He discovered that in the passerines and *Upupa* “. . . the tendon of the *flexor longus hallucis* muscle is quite independent of that of the *flexor perforans digitorum*; whilst in other birds the former joins the latter, so preventing the two from being quite independent in their action” (Garrod, 1875: 340). The later discovery of a vinculum between the two tendons in the Eurylaimidae (Garrod, 1877b) somewhat modified this definition but the disposition of the deep plantar tendons became an important character in classification when Garrod (1875) extended his observations to other groups of birds. He described the arrangement of these tendons in many species and found a vinculum between them in all except the passerines, *Upupa*, *Botaurus stellaris* and *Ardea cinerea*.

Of particular interest was Garrod's discovery of two different arrangements of the deep plantar tendons in birds with zygodactyl feet. Furthermore, the two plantar tendon types correlated with the presence or absence of the ambiens muscle which was the basis for Garrod's two suborders. One can imagine Garrod's delight in finding these correlations, which led him to conclude that “these new observations are therefore strongly in favour of the naturalness of the classification proposed” (1875: 347). Garrod had discovered that the parrots and cuckoos (including the turacos) have the ambiens (= Homalagonatae), and also agree in the arrangement of their deep flexors and that the anomalognatous Picidae, Ramphastidae, Capitonidae, Bucconidae, and Galbulidae possess a different deep flexor pattern. Although Garrod's confidence in his two groups based on the ambiens was not shared by his successors the groupings based upon the deep plantar tendons have persisted to the present day.

Gadow and Selenka (1891: 195) described seven patterns of insertion of the deep plantar tendons and Gadow (1894: 615-18) listed eight major types with several variants for a total of 15 patterns. A vinculum was also found in *Upupa* by Gadow.

Beddard (1898a: 178, footnote) noted that the plantar vinculum is occasionally absent in *Calyptomena viridis* and Pycraft (1905) considered the deep plantar tendons to be of doubtful taxonomic value in the classification of the broadbills.

Mitchell (1901c) examined the deep plantar tendons in 17 species of kingfishers and found 10 different variants. (See under Coraciiformes for additional comments on this subject.)

W. D. Miller (1919) confirmed the findings of Garrod on the deep plantar tendons in the jacamars and puffbirds. Miller dissected additional species of several piciform families and found all to be “antiopelmous” (= Gadow's Type VI) as Garrod had claimed. Miller also affirmed his belief in a close relationship among the families possessing “antiopelmous, zygodactyl feet” and noted: “As this character is not neutralized or overbalanced by any of equal or greater value we may regard these families as forming a natural group, an order or suborder . . .” (p. 286).

The most recent review of the conditions of the deep plantar tendons is that of J. George and Berger (1966: 447-49), who updated and annotated Gadow's eight major patterns as follows:

Type I. The flexor hallucis longus tendon inserts on the hallux; the flexor digitorum longus tendon trifurcates, sending branches to digits II, III, and IV. The vinculum passes downward from the hallucis tendon and fuses with the flexor digitorum tendon; hence, the flexor hallucis longus muscle aids in flexing all of the toes. This pattern is found in many birds: for example, *Columba*, Ardeidae, Ciconiidae, Galliformes, many Gruiformes and Charadriiformes, Psittacidae, Musophagidae, Cuculidae, and Eurylaimidae.¹ Hudson *et al.* (1959)

¹ Olson (1971) has reviewed the condition of the vinculum in the Eurylaimidae and concludes that it is too variable to be used as the basis for the subordinal separation of the group.

reported considerable variation in the development of the vinculum among genera of galliform birds.

Type II. This type is like Type I except that most of the flexor hallucis longus tendon becomes the vinculum and fuses with the tendon of *M. flexor digitorum longus*. Only a small part of the hallucis tendon continues distad to insert on the hallux. This pattern is found in the Spheniscidae, *Apteryx*, Tinamidae, Pelecaniformes, Anhimidae, Anatidae (Gadow).

Type III. The two deep plantar tendons are "more or less fused throughout the greater extent" of the tarsometatarsus but the vinculum passes from the distal portion of the hallucis tendon to the branch of flexor digitorum longus which goes to digit II only. This pattern is found in *Sagittarius*, the Accipitridae, *Falco*, and *Polihierax* (Hudson, 1948; Berger, 1956).

Type IV. The entire tendon of *M. flexor hallucis longus* fuses with the tendon of *M. flexor digitorum longus*. The combined tendon trifurcates and sends branches to digits II, III, and IV; no branch is sent to the hallux. This pattern is found in tridactyl birds and those in which the hallux is small: for example, *Rhea*, *Casuaris*, *Dromiceius*, *Gavia*, *Podiceps*, Procellariiformes, *Phoenicopteris*, some Anhimidae, *Turnix*, and *Pterocles* (mostly after Gadow).

Type V. The entire tendon of *M. flexor hallucis longus* fuses with the tendon of *M. flexor digitorum longus*. The common tendon then gives rise to four branches, which supply all four toes (e.g., *Fregata*, Cathartidae, *Pandion*, *Chordeiles*, *Chaetura*, *Apus*, *Colius*, *Buceros*, *Aceros*). Neither Fisher (1946) nor Hudson (1948) found the elaborate branching to the toes in the Cathartidae described by Gadow. In *Coracias abyssinica* the tendon of flexor hallucis fuses with the lateral margin of the tendon of flexor digitorum in the distal fourth of the tarsometatarsus. The combined tendon then sends branches to all four toes, but there is no crossover of the tendons visible grossly; the tendon of *M. flexor hallucis longus* contributes to that part of the combined tendon that supplies digit IV and the hallux.

An "exaggerated condition" of this type is found in todies, motmots, bee-eaters, and some kingfishers, in which the tendon to the hallux arises a short distance superior to the fusion of the two deep plantar tendons (Gadow). Hudson (1937) describes a similar pattern in *Chen* and *Mergus*.

Gadow describes a third modification in the Trochilidae, in which the tendon of flexor hallucis longus supplies digits I and IV and the tendon of the flexor digitorum longus supplies digits II and III.

An apparently previously unrecorded pattern is found in *Chloroceryle americana*. The tendon of *M. flexor digitorum longus* supplies all four digits; the tendon bifurcates just inferior to the hypotarsus. The medial branch supplies the hallux; the larger lateral branch trifurcates at the level of metatarsal I and supplies digits II, III, and IV. *M. flexor hallucis longus* does not send a branch to the hallux. The tendon bifurcates and sends branches, which join similar branches of the digitorum tendon, to digits III and IV only.

Type VI. The tendon of *M. flexor digitorum longus* is reinforced by a vinculum and inserts on digit III only. The tendon of *M. flexor hallucis longus* sends a vinculum to the digitorum tendon and also sends branches to insert on the hallux and on digits II and IV. By means of the vinculum, therefore, the hallucis tendon acts on all four toes. This pattern is found in the Piciformes (Galbulidae, Bucconidae, Capitonidae, Indicatoridae, Ramphastidae, Picidae, Jyngidae). Berger found this configuration of tendons in *Indicator variegatus*.

Type VII. The deep plantar tendons are independent throughout; a vinculum is absent. The flexor hallucis tendon inserts on the hallux only. The flexor

digitorum trifurcates and inserts on digits II, III, and IV. This pattern is characteristic of the Passeriformes (except the Eurylaimidae). Berger found this pattern in the cotinga, *Procnias nudicollis*.

Type VIII. The tendon of the flexor digitorum longus, reinforced by a large vinculum from the hallucis tendon, inserts on digits III and IV only. The flexor hallucis tendon bifurcates to supply digits I and II; the vinculum goes to that part of the flexor digitorum tendon that inserts on digit III. This pattern is found only in the heterodactyl Trogonidae. Berger can verify this pattern in *Pharomachrus mocino*.

The questions are: (1) How consistent are these patterns of the deep plantar tendons within groups? (2) Can we be certain that the deep plantars, as Miller (1919) claimed, are indicative of natural groups?

At least two facts should be considered in evaluating the deep plantar tendon patterns. First, Gadow (1894: 618) noted that Types I, II, III, IV and VII "are closely allied to each other; I. and IV. to be derived from II. and VII. from I., while III. is a comparatively primary condition; V,a shows a primitive stage, whence are developed in diverging directions V,b, V,c, V,d, VI. and VII. Any derivation of VI. from VIII. or *vice versa* is impossible; and the same applies to V,c and VI." Second, Mitchell (1901c) found an enormous amount of variation among the kingfishers.

The possible derivations noted by Gadow indicate that the condition in the Piciformes (Type VI) could have been derived from the pattern found in the Coraciiformes (Type Va,b) and the great variation found in the kingfishers suggests that there is nothing highly restrictive about the adaptive potential of the deep flexor tendon patterns. Instead of viewing these patterns as diagnostic of the Piciformes, which is possibly an exercise in circular reasoning, it is at least equally valid to view them as merely another variable adaptive character that responds readily to the demands of natural selection. So viewed it is possible to see the Type VI tendons of the jacamars and puffbirds as another variant of the many kingfisher patterns rather than as proof that the Galbulae are piciform. Also consistent with this view is the range of taxa which share little more than Type I, Type II, Type IV or Type V patterns as noted above.

4. CONVOLUTIONS OF THE INTESTINAL TRACT

Although a number of earlier workers published observations on the intestinal tract in birds (see Beddard, 1910: 48) it was Gadow (1879, 1889) who first developed a scheme for using the convolutional pattern of the small intestine as a taxonomic character. Gadow (1889) examined more than 300 species representing "nearly every principal family" (p. 304) and presented a set of diagrams illustrating the principal patterns. Two main types, "orthocoelous" and "cyclocoelous," were identified. Of the orthocoelus condition Gadow noted four main variants and two additional sub-variants. Brief descriptions of these coiling patterns follow.

A. CYCLOCOELOUS. Some of the intestinal loops form a spiral. The terms "telogyrous" and "mesogyrous" were used to describe variants of the spiral pattern.

B. ORTHOCOELOUS. Intestine forms a number of loops which run parallel to one another in the long axis of the body.

1. Isoceolous. Second and subsequent loops closed and left-handed. Ascending branch of one loop runs side by side with descending branch of next loop.

2. Anticoelous. Second loop closed and left-handed, third loop closed and right-handed.

3. Plagiocoelous. At least second loop, which is generally open, doubled over in horseshoe shape.

4. Pericoelous. Second loop open, left-handed and surrounding third loop, which is generally straight and closed. "This formation is of especial interest because it leads quite gradually to the" cyclocoelous pattern (Gadow, 1889: 305).

Two sub-variants were designated "anti-pericoelous" and "iso-pericoelous."

Gadow described the intestinal convolutions in many groups and made comparisons among them. He noted several additional modifications of the named patterns and he found that many of the similarities between groups "are perhaps merely coincidences, and in this case can have no taxonomic significance; but if these similarities coincide with those of several other organic characters, they are entitled to a higher rank as indicating not convergence but common descent of those birds in which they persistently occur" (1889: 307).

Forbes (1880c) strongly disagreed with some of the assemblages proposed by Gadow (1879). Forbes noted that within the group with a "mesogyrous" coiling pattern are the falconiform genera *Accipiter* and *Melierax*, the kingfisher *Halcyon* and the flamingo *Phoenicopterus*. He wrote:

It seems to me that, as it is a well known fact that individuals of the same species vary, sometimes very greatly, in the length of their intestines, the stowing away of a greater or less amount of gut in a given space, the abdominal cavity, becomes simply a mechanical problem, and therefore there is less help in forming a sound view of the mutual affinities of birds to be derived from the facts in this direction described by Dr. Gadow than from many other points, more complicated, and therefore less easily altered, in the structure of birds" (p. 236-37).

Forbes' objection was valid, for it is possible to find both consistency and inconsistency in Gadow's data. Within the Charadriiformes some "Limicolae" are pericoelous, others cyclocoelous. Some Laridae are pericoelous, others cyclocoelous; some Alcidae are amphicoelous, others cyclocoelous. Several types of convolutions occur within the Falconiformes, Procellariiformes and Ciconiiformes but the Passeriformes "are a very uniform group" (p. 315).

Gadow was fully aware of the relationship between food habits and the structure of the digestive tract but he also thought that dietary modifications often affected the caeca, crop and stomach rather than the pattern of intestinal coiling (e.g., p. 310). The similarities between parrots and hawks in coiling pattern (telogyrous), presence of a crop and absence of functional caeca was a difficulty Gadow could not explain, for he discounted a relationship between them (p. 313).

Gadow and Selenka (1891: 707-709) described eight pattern types and listed the groups of birds having each pattern. Some of the groups are convincing (e.g., rails, shorebirds, pigeons) but others (herons, hawks, parrots) are not.

Mitchell (1896) introduced his first long paper on the avian intestinal tract by stating that Gadow "has . . . proved the taxonomic value of the intestinal convolutions in birds . . ." (p. 136). Mitchell included the mesenteries and veins in his study and began with the assumption that the simple condition in *Alligator* was the "ground-type." He then described the variations he found in birds.

Mitchell agreed and disagreed with Gadow on various points and concluded (p. 159) that "in these loopings of the gut in birds, there is an almost kaleidoscopic variety, and apparently these varieties are of systematic value; what are their utilities?"

This rather cryptic final remark apparently meant that Mitchell wasn't certain just how to interpret the variation he had encountered.

Beddard (1898a: 23-30) reviewed the papers by Gadow and Mitchell but did not present his opinion as to the taxonomic value of the intestinal convolutions. However, he did include data on intestinal patterns in his discussions of the group of birds.

Mitchell (1901a) soon published an expanded study of the avian intestinal tract based upon "many hundreds of birds, including a number of rare forms, and representing nearly all the important groups of birds" (p. 175). He took the condition in the Horned Screamer (*Anhima cornuta*) as his starting point because it seemed to him to represent the "primitive, ancestral, or central condition, from which the conditions found in the other cases have diverged" (p. 178). Mitchell called this pattern "archecentric" and the modified conditions "apocentric." He then introduced definitions of four "homoplastic modifications" of the gut and coined several other terms to describe other conditions and to organize a scheme which he believed described the evolutionary pathways of the avian intestinal tract. These terms and Mitchell's arguments are largely irrelevant to the taxonomic evaluation of his data. Mitchell presented diagrams which summarized his ideas as to the "relations of the intestinal tracts, and not necessarily the relations of the possessors of these tracts" (p. 270). He thus avoided a confrontation between his intestinal tract data and that from other sources.

It was Beddard (1910) who finally evaluated the intestinal tract patterns in taxonomic terms. He was critical of the methods of both Gadow and Mitchell, noting that the latter oversimplified the actual variation "with the result that birds which are separated by marked characters are represented as being almost identical" (p. 49-50). Beddard described the intestinal tract in an additional number of species and came to the general conclusion that although the facts concerning the intestinal convolutions do not "permit of any complete scheme of classification" (p. 89) there are indications of relationship in some cases. Within some groups all species have a nearly identical intestinal pattern. Thus all parrots are alike as are the Galliformes, Falconiformes and Strigiformes. However, the members of other groups diverge greatly from one another as in the "Picopasseres, Limicolae, Grues, [and] Struthionies" (p. 93).

And, finally, Beddard concluded (p. 89) that "certain classificatory results seem to follow from a comparison of the differences exhibited by the intestinal tract. Thus, the resemblance of both Cuculi and Musophagi to the Picopasseres, and the likeness between all the Accipitres (New World and Old World, nocturnal and diurnal) are remarkable. The close likeness between the Bustards and the Cariamidae is to be commented upon. The passerine character of the gut of *Turnix* and the possible likeness between *Crypturus* and *Rhea* seem also to be shown."

Since today several of these "classificatory results" can be shown to be wrong or doubtful it seems reasonable to conclude that the taxonomic value of the intestinal convolutions is virtually nil.

5. THE CAROTID ARTERIES

Garrod (1873b) was the first to make extensive use of the arrangement of the carotid arteries as a taxonomic character. He examined 400 species representing some 300 genera and described four principal patterns:

- 1) Two carotids of equal size which run up the neck and enter the hypopharyngeal canal, running side by side but separate. Present in many groups of birds.
- 2) The left carotid only developed. In all Passeriformes and several other groups.

3) The right carotid artery present in its normal position in the hypapophysial canal but the left superficial in company with the left jugular vein and vagus nerve. Present in some parrots.

4) The two carotid arteries merge and a single artery runs in the hypapophysial canal to the head. Variation in the size of the two trunks. Of equal size in *Botaurus*, the right larger in *Phoenicopterus*, the left larger in *Cacatua*.

Garrod (1874c) found a fifth condition in the bustard *Eupodotis* in which only the right carotid is present. Garrod (1876a) and Otley (1879) found that in *Bucorvus* both carotids are reduced to fibrous imperforate cords, their vascular function having been assumed by other vessels.

Forbes (1881d: 7) reviewed Garrod's work and concluded that ". . . the disposition of the carotid arteries has not much significance amongst birds, there being many families in which, whilst the majority of the species have two, some have only one carotid." Forbes cited several such cases including *Tockus* and *Bucorvus* (Bucerotidae), *Anhinga* and *Phalacrocorax* (Phalacrocoracidae) and *Apus* and *Cypseloides* (Apodidae). "In other cases, . . ." Forbes noted, "the characters of the carotids hold good through very large groups: thus no Passerine bird has ever yet been found with more than a left carotid, and no Pigeon, Duck, or Bird of Prey without two normally placed ones."

Forbes (1882f) found a modification in the passerine *Orthonyx* (Timaliidae) in which the left carotid runs superficially rather than in the hypapophysial canal.

Beddard (1898a: 54), after reviewing the work of Garrod, Forbes and others on the carotids, concluded that "these facts, striking though they are, are unfortunately of but little value in classification, or at least their value is not understood."

The next important studies of the carotid pattern were those of Glenny, who published a series of some 40 papers beginning in 1940. In 1955 he summarized this work, and included a bibliography of his own papers. Glenny (1955: 527) stated that "even Forbes and Beddard failed to interpret Garrod's studies satisfactorily, . . ." and expressed his belief that further extensive embryological studies will be necessary before the various patterns in adult birds can be interpreted.

Glenny described four major bicarotid patterns and six major unicarotid patterns, with additional modifications in each group. Using a coded system he set up a series of 5 bicarotid arrangements and 15 unicarotid arrangements to cover all possible conditions, some of which have not yet been discovered. Following is Glenny's classification of carotid arrangements based upon his 1955, 1957, 1965 and 1967 papers. Unless otherwise indicated the data are from the 1955 review.

CLASS A—TWO CAROTIDS

A-1. Bicarotidinae normales. The two dorsal carotids enter the hypapophysial canal and pass anteriorly to the head without fusing. This is the basic arrangement from which all others have been derived. It is found in at least some species in most orders of birds although exclusively only in the following: Struthioniformes, Casuariiformes (Glenny, 1965), Tinamiformes, Sphenisciformes, Gaviiformes, Anseriformes, Falconiformes, Columbiformes, and Strigiformes. The Casuariiformes are mostly A-1 but some *Casuaris* are not; most Procellariiformes are A-1, but a few are unicarotid; all Galliformes except the Megapodiidae and all Gruiformes except the Heliornithidae, Turnicidae and some Otididae are A-1. The Charadriiformes except for some Alcidae and the Caprimulgiformes except the Podargidae and Nyctibiidae are A-1. Some Psittaciformes are A-1 (Glenny, 1957).

A-2-d. Bicarotidinae abnormales: right vessel superficial. No examples.

A-2-s. Bicarotidinae abnormales: left vessel superficial. Uncommon, found in many parrots (Glenny, 1957).

A-3. Bicarotidinae infranormales: both vessels superficial. Rare, known only in certain cuckoos (*Zanclotomus*, *Phaenicophaeus*). In *Rhamphococcyx* the left dorsal carotid serves as a reduced ascending oesophageal artery, the right carotid is a small ligament. Coded by Glenny (1955: 583) as A-3-s/A-4-d.

A-4. Ligamenti carotidinae normales (ligamenti ottleyi). Both dorsal carotids atrophied. Function taken over by other vessels. Rare, known only in *Bucorvus* (Bucerotidae) and *Rhopodytes* (Cuculidae).

CLASS B—ONE CAROTID

B-1. Conjuncto-carotidinae normales. Single carotid in the hypapophysial canal, formed from two vessels of equal size. Found only in the Ciconiiformes, where it is quite inconsistent even within genera and species, e.g., most *Ardea* are A-1 but *A. herodias treganzai* is B-1 while *A. h. herodias* is A-1. *Butorides virescens* is B-1, *B. sundevalli* is A-1; *Ixobrychus minutus* and *I. sinensis bryani* are A-1 but *I. s. sinensis* is B-1. Thus, carotids in the Ardeidae are variable.

B-2-d Conjuncto-carotidinae abnormales. Right side reduced. This condition like B-1 but the right carotid smaller than the left. Found in *Kakatoe*² *sulphurea* (Psittacidae) (see Glenny, 1957) and *Podargus ocellatus* (Podargidae). Other Podargidae are B-4-s and other *Kakatoe* are B-3b-d.

B-2-s Conjuncto-carotidinae abnormales. Left side reduced. In some herons (*Ardeola speciosa*; some specimens of *Botaurus lentiginosus*), the flamingos, perhaps in *Kakatoe* (see Glenny, 1955: 580). *Megapodius nicobariensis* is B-2-s, other megapodes are B-4-s or B-3b-d.

B-3a-d Ligamentum carotidinae-conjuncti: partial lumen; ligament on right side. In a specimen of *Priocella antarctica* (Procellariidae) and in *Tockus* (Bucerotidae).

B-3a-s Ligamentum carotidinae-conjuncti: partial lumen; ligament on left side. No examples given by Glenny (1955).

B-3b-d Ligamentum carotidinae-conjuncti; entire, on right side. Found in Pelecanidae, *Megapodius pritchardii* (but not other megapodes), *Chaetura vauxi*, *Chaetura cinereiventris* and *Tachornis phoenicobia* (Apodidae), and *Kakatoe galerita*, *leadbeateri* and *sanguinea* (Psittacidae). See *K. sulphurea* above under B-2-d. See Glenny, 1957, for details.

B-3b-s Ligamentum carotidinae-conjuncti: entire, on left side. No examples.

B-4-d Dextro-carotidinae normales: right carotid alone enters hypapophysial canal. Found in *Eupodotis* (Otididae), but other bustards are A-1; also reported in a barbet (Capitonidae) but other barbets are B-4-s.

B-4-s Laevo-carotidinae normales: left carotid alone enters hypapophysial canal. This arrangement in many groups: Rheiformes, Apterygiformes (Glenny, 1965), Podicipediformes, Coliiformes, Trogoniformes, Piciformes (except the barbet above under B-4-d), Passeriformes (except *Orthonyx* [Timaliidae], which is B-5-s), *Anhinga*, *Balaeniceps*, Turnicidae, Nyctibiidae, *Hemiprocne*, Trochilidae, Upupidae, Phoeniculidae, some Apodidae (varying within genera), most Podargidae, most Megapodidae (but others B-2-s or B-3b-d). One specimen of *Casuaris* (Glenny, 1955: 553) was B-4-s, others are A-1. A specimen of *Pelecanoides garnoti* was B-4-s, others are A-1 (Glenny, 1955: 557), *Sula* is B-4-s, *Morus* is A-1 (Sulidae), *Fregata aquila* A-1, *F. minor* B-4-s (Glenny, 1955: 558), most Alcidae are A-1 but *Plautus alle* and five specimens of *Synthliboramphus antiquum* were B-4-s. Two specimens of *S. antiquum* and two of *S. wumizusume* were A-1 (Glenny, 1955: 576). Most bee-eaters (Meropidae) are B-4-s but *Melittophagus* is A-1.

B-5-d Dextro-carotidinae infranormales: right carotid is superficial, left is lacking. No examples.

² *Kakatoe* has been replaced by *Cacatua*. See Mayr, Keast, and Serventy, 1964.

B-5-s Laevo-carotidinae infranormales; left carotid is superficial, right is lacking. Known only in the timaliid genus *Orthonyx*.

B-6a-d Ligamentum unicarotidinae (ligamentum ottleyi): entire, right side. No examples.

B-6a-s As above, left side. No examples.

B-6b-d Ligamentum unicarotidinae: incomplete or lacking, right side. No examples.

B-6b-s As above, left side. No examples.

The B-6 series represents Glenny's assumption of what might result from further atrophy of the unicarotid condition. Other arteries would take over the function of the carotids.

It seems obvious that the numerous exceptions and special cases render the adult carotid artery patterns virtually useless as a basis for a general classification of the higher categories. Glenny is probably correct in his belief that only extensive embryological studies will clarify the situation. Certainly, the data available to Gadow in 1892 cannot now be considered to have been reliable.

6. THE FIFTH SECONDARY

Although Gerbe (1877) first noticed that some birds apparently lack a fifth secondary, it was Wray (1887) who brought the condition to the attention of taxonomists. The gap in the secondaries was detected because a greater covert is present between the fourth and sixth secondaries but no secondary is present at the corresponding position. It was therefore assumed that the fifth secondary was missing, and birds lacking the fifth secondary were termed "aquintocubital." Birds having a fifth secondary were called "quintocubital." Later Mitchell (1899) suggested the substitution of "diastataxic" and "eutaxic" for these conditions.

The taxonomic value of the presence or absence of the fifth secondary was quickly investigated and its significance debated. Various authors (e.g., Gadow, 1888; Sclater, 1890; Goodchild, 1886, 1891; Pycraft, 1890; Gadow and Selenka, 1891; Degan, 1894; Seebohm, 1895; Mitchell, 1899; Pycraft, 1899c; Mitchell, 1901c; W. D. Miller, 1915, 1924; Steiner, 1946, 1956, 1958) assembled data on the fifth secondary in many groups of birds.

W. D. Miller (1924) and Steiner (1956, 1958) reviewed the earlier work, added to it, corrected several errors and presented useful summaries upon which the following lists are based.

A. ALL OR MOSTLY DIASTATAXIC

Archaeornithes (*Archaeopteryx*)
 Casuariiformes (Emu, Cassowaries)
 Gaviiformes (Loons)
 Podicipediformes (Grebes)
 Sphenisciformes (Penguins)
 Procellariiformes (Petrels, Albatrosses)
 Pelecaniformes (Pelicans, Cormorants, etc.) except *Nannopterum*
 Ciconiiformes (Hérons, Storks, Flamingos)
 Anseriformes (Ducks, Geese, Screamers)
 Falconiformes (Hawks, Vultures, Falcons)
 Pedionomidae (Plains-wanderers)
 Gruidae (Cranes)
 Aramidae (Limpkins)

Eurypygidae (Sunbitterns)
 Otididae (Bustards)
 Charadriiformes (Shorebirds) except *Philohela*
 Pteroclididae (Sandgrouse)
 Psittaciformes (Parrots)
 Strigiformes (Owls)
 Hemiprocnidae (Crested-swifts)
 Caprimulgiformes (Goatsuckers)
 Coraciidae (Rollers)
 Leptosomatidae (Cuckoo-rollers)

B. GROUPS CONTAINING BOTH EUTAXIC AND DIASTATAXIC FORMS

Except for the Rallidae, the Gruiformes of Wetmore (1960) separate into eutaxic and diastataxic groups on family lines and are so listed above and below. The rails, pigeons and kingfishers are especially complex and some additional comments on these groups are presented below.

Megapodiidae (Megapodes). *Megapodius* and *Megacephalon* diastataxic; *Leipoa* and *Alectura* eutaxic.

Columbidae (Pigeons). See below.

Rallidae (Rails). See below.

Charadriiformes (Shorebirds). Diastataxic, except *Philohela*.

Turnices (Bustardquails). *Pedionomus* is diastataxic, *Turnix* and *Ortyxelos* eutaxic.

Pelecaniformes (Pelicans, Cormorants, etc.). All are diastataxic except the flightless cormorant, *Nannopterum*.

Alcedinidae (Kingfishers). See below.

Apodidae (Swifts). "Chaeturinae" variable. "Micropodinae" eutaxic. See W. D. Miller (1924: 310).

Trochilidae (Hummingbirds). Diastataxic except *Glaucis hirsuta*, *Phaethornis guy* and *Eutoxeres aquila*. The unique type specimen of *Eucephala caeruleo-lavata* Gould (= *Cyanophaia caeruleolavata*) is eutaxic in one wing, diastataxic in the other (Miller, 1924: 311). Peters (1945: 48-9) considered this specimen to be "almost certainly" a hybrid.

Brachypteraciidae (Ground-rollers). See Steiner, 1956: 19.

C. ALL OR MOSTLY EUTAXIC

Struthioniformes (Ostrich)
 Rheiformes (Rheas)
 Tinamiformes (Tinamous)
 Galliformes (Pheasants, Grouse, etc.) except some megapodes.
 Mesitornithidae (Roatelos, *Monias*)
 Turnicidae (Bustardquails)
 Psophiidae (Trumpeters)
 Heliornithidae (Sungrebes)
 Rhynochetidae (Kagus)
 Cariamidae (Seriemas)
 Cuculiformes, including *Opisthocomus* (Cuckoos, Turacos)
 Coliiformes (Colies)
 Trogoniformes (Trogons)
 Coraciiformes (Kingfishers, Bee-eaters, Motmots, etc.) except the rollers and some kingfishers.
 Piciformes (Woodpeckers, Barbets, Toucans, etc.)

Passeriformes (Perching Birds)

Rallidae. Most rails are diastataxic but Miller (1924: 309) listed eight eutaxic species. In at least two genera, *Creciscus* and *Sarothrura*, both conditions are found. And in some *Sarothrura* both conditions are present within a single species. Miller (p. 308) concluded that "the taxonomic value of this feature in *Sarothrura* is comparable to that of the relative development of the tenth primary in *Vireosylva* and *Lanivireo*."

Columbidae. Mitchell (1899) found that most pigeons are diastataxic but he discovered seven eutaxic species. Bates (1918) added several more and Miller (1924: 306-07) presented a list of 36 diastataxic and 20 eutaxic species. All of the eutaxic forms were members of the "Peristeridae," which included such genera as *Geopelia*, *Scardafella*, *Columbina*, *Chamaepelia*, *Claravis*, *Tympanistra*, *Turtur*, *Phaps*, *Ocyphaps*, *Gallucolumba* and *Starnoenas*. Other genera of the "Peristeridae" were listed as diastataxic, including *Zenaida*, *Zenaidura*, *Streptopelia*, *Oena*, *Chalcophaps*, *Leptotila*, *Oreopeleia* and *Caloenas*. All members of the "Treronidae" and "Columbidae" were found to be diastataxic. The complications extend beyond these bare lists. (See Miller, 1924: 307, and Steiner, 1956: 14-15.)

Alcedinidae. The kingfishers include both conditions. Using names corrected to Peters (1945) the following summarizes the findings of Mitchell (1901c):

1) Eutaxic species: *Halcyon pileata* (but with vestige of "old diastataxic condition"); *Halcyon coromanda rufa*; *Chloroceryle americana*; *C. inda*; *Cittura cyanotis* (including *C. c. sanghirensis*); *Alcedo meninting* (= *A. asiatica*); *A. atthis* (including *A. a. ispida* and *A. a. bengalensis*); *Ceyx rufidorsa*.

2) Diastataxic species: *Dacelo novaeguineae*; *Halcyon chloris* (including *H. c. sordida*); *Halcyon sancta* (including *H. s. vagans*); *Ceryle maxima*, and *C. alcyon*.

Mitchell (1901c: 102-03) commented that "the seventeen Kingfishers which I have examined thus show plainly that here, as in the Columbidae, the conditions known as eutaxy and diastataxy cannot be regarded as fundamental characters in any of the greater schemes of classification. Both conditions occur, scattered as it were indiscriminately within the confines of the group, and sometimes even within the confines of a genus. Nor are the two conditions absolutely marked off one from another, but lend themselves to an arrangement in a graded series, which suggests the production of one condition as a simple modification of the other."

By the examination of other characters Mitchell tried to show that the eutaxic pigeons (1899) and kingfishers (1901c) are the more "specialized." The attempt fails because it depends upon Mitchell's subjective definition of "primitive" and "specialized" in each example.

Pycraft (1899c: 254) discussed diastataxy as a factor in classification and noted that a division of the Aves into two groups of eutaxic and diastataxic birds was impossible but he thought that the condition of the fifth secondary could be used within groups. ". . . The presence of diastataxy in a little coterie of forms, admittedly related, but hitherto indiscriminately mixed with eutaxic, will . . . justify our separating them . . . on the assumption . . . that they are . . . more closely related one to the other than to the neighbouring eutaxic forms." But the mixed groups made it necessary for Pycraft to propose a theory for which there was no evidence, let alone proof. He wrote (p. 254): "The presence of discordant elements in the shape of eutaxic forms amongst our now diastataxic groups—such as the Kingfishers, Swifts, and Pigeons—must be attributed to reversion or secondary readjustment of the feathers resulting once more in eutaxy. This is not as convincing as it should be; but it demands less of us than the alternative hypothesis, that diastataxy has been independently acquired wherever it occurs."

It was Steiner (1917, 1946, 1956, 1958) who worked out the embryological basis of diastataxy and provided the most likely explanation for the seemingly haphazard distribution of the condition of the fifth secondary. Steiner (1956) argued that diastataxy is the primitive condition and that eutaxy has been derived from it, independently, in various groups of birds. Steiner reinvestigated the condition in *Archaeopteryx* and, in opposition to DeBeer (1954), found it to be diastataxic.

Steiner's (1956) description of the development of the secondaries in a diastataxic wing is as follows (p. 5, transl.). The earliest secondary feather germs appear on the ulnar margin of the forearm. They form as small round buds (papillae) and occur in two separate rows, one that begins proximally near the elbow and a second which is located distally and extends to the wrist. It is clear that there are two separate rows, the proximal extends above the distal and the distal row extends below the proximal to the elbow. This observation provides the explanation for the development of diastataxis; the secondaries which insert on the margin of the wing in recent birds have developed from two separate rows of feathers situated on the forearm. The proximal half of the secondary series originated from the upper row, the distal half from the lower row. Accordingly, the secondary coverts are arranged in gradually rising transverse rows and are displaced along the forearm to the extent of one longitudinal series of feathers. The place of transition from the proximal portion of the row to the distal portion is at the fifth and sixth cross-rows respectively. Thus here the feathers have intermediate positions and the fifth secondary does not develop. In eutaxic birds the feather germs also develop in two rows, one proximal, the other distal. The early stages are like those of the diastataxic wing but very soon the eutaxic wing begins to develop in a different fashion.

Steiner found that in the mixed groups (doves, kingfishers, etc.) it is possible to find developmental stages intermediate between eutaxy and diastataxy. He concluded that a eutaxic wing is correlated with the need for a strong "rowing wing" as in tree-, brush-, and ground-dwelling birds or in marsh and water birds that must fly without a running start. Furthermore, in the embryos of ostriches and rheas (Steiner, 1946), which are eutaxic, it is possible to see evidence of the earlier diastataxic condition. The diastataxic wing tends to be present in long-winged birds which do not live in dense vegetation or have to fly upward to escape predators.

Steiner (1956: 14-16) concluded that the taxonomic significance of diastataxy is as a character that indicates the "primitive" species in the mixed groups where both conditions occur and which therefore can be important in the phyletic understanding of such groups.

We conclude that the taxonomic value of diastataxy is limited. The wide occurrence of each condition in unrelated forms and the variation within closely related groups of species indicates, as Steiner noted, that it is adaptive and of taxonomic value only to bolster other evidence and then only in special cases. As a character in higher category classification it should be viewed with distrust.

SUMMARY

We think the point has been made. These six characters are all taxonomically useful to some degree but none of them is completely consistent and trustworthy. We are not the first to make this suggestion; indeed, the original authors in every case were aware of the shortcomings, but their successors have not always been as wary. We believe that all of Gadow's 40 characters can be shown to suffer from the same disabilities and that the reason is simply that all are adaptive and therefore subject to convergence. This does not mean that they are devoid of taxonomic information, only that they must be interpreted with caution.

THE EGG WHITE PROTEINS

Nearly all chemical studies on egg white proteins have dealt with those of non-passerine birds. Thus, we have more confidence in our understanding of non-passerine protein homologies than in those of passerines. Other data (e.g., on the occurrence and extent of electrophoretically detectable polymorphisms within a species) aid in interpreting the starch gel patterns. A summary of information about the main protein fractions visible in the starch gel patterns is therefore appropriate.

As many as 22 fractions in chicken egg white (C. Baker and Manwell, 1962) have been separated using starch gel electrophoresis. Some of these are poorly characterized or as yet unidentified. About six principal components appear in the starch gel patterns of all avian egg whites and are of greatest importance in the evaluation of the patterns. The general physical and chemical properties of the main egg white proteins have been discussed in detail by Fevold (1951) and Warner (1954) and in review by Sibley (1960), Feeney (1964), and C. Baker (1968). Tristram and Smith (1963: 307) and Feeney and Allison (1969) gave amino acid compositions for several other egg white proteins as well, and from a number of species. The volume edited by Gottschalk (1966) gives information on the chemistry of glycoproteins, including ovalbumin, ovomucoid, and conalbumin.

Recent unpublished studies by the present authors using the technique of "isoelectric focusing" in acrylamide gels have separated as many as 30 proteins in some species. In the ostrich (*Struthio camelus*) 35 protein bands have been detected. Vesterberg (1971) and Wrigley (1971) have reviewed the isoelectric focusing technique.

Board (1970) reviewed the microbiology of the chicken (*Gallus gallus*) egg, particularly with regard to the agents and mechanisms of bacterial infection of eggs. Other aspects of the avian egg and embryonic development are treated in the books by Romanoff and Romanoff (1949, 1967) and A. L. Romanoff (1960).

The major features of the starch gel pattern, which will be referred to under each family account, are described below and diagrammatically represented in Figure 1. It is hoped that these will enable one to follow the discussion more readily and to understand the patterns depicted in the plates.

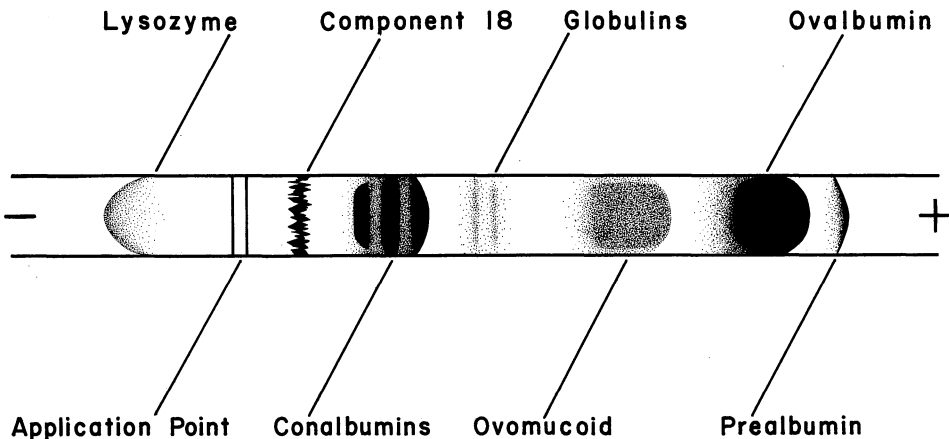


FIG. 1. Diagram of the starch gel electrophoretic pattern of the egg white proteins of a non-passerine bird. The (+) indicates the anodal direction, the (-) the cathodal direction. Conalbumins = transferrins; they may move anodally or cathodally from the application point. Component 18 = ovomacroglubulin.

LYSOZYME

Migrating toward the cathode (i.e., to the left of the application slot) is lysozyme, which appears characteristically as a crescent-shaped band. It is most readily observed in patterns of the Galliformes (figs. 16–18), although in this group the concentration varies from species to species (Feeney et al., 1960). In other avian taxa it may be present in amounts too small to be detected by staining. Lysozyme is best known for its ability to hydrolyze β -1, 4-glycosidic linkages in the mucopolysaccharide walls of bacteria (Boasson, 1938; Smolelis and Hartsell, 1949; review by J. Jollès et al., 1963). The molecule contains 129 amino acid residues and has a molecular weight of about 14,600.

Amino acid sequences or compositions of the egg white lysozymes have been determined for the chicken (*G. gallus*) (Canfield, 1963a,b; Canfield and Anfinson, 1963), turkey (*Meleagris gallopavo*) (LaRue and Speck, 1970), Old World quail (*C. coturnix*) (Kaneda, et al., 1969), mallard duck (*Anas platyrhynchos*) (Hermann and Jollès, 1970) and domestic goose (*A. anser*) (Canfield and McMurry, 1967; Kammerman and Canfield, 1969) and the black swan (*Cygnus atratus*) (Arnheim and Steller, 1970). (See Galliformes section for further details). The disulfide bonding (Canfield and Liu, 1965) and three-dimensional structure of chicken lysozyme (Blake et al., 1962; Dickerson et al., 1962) have also been determined in considerable detail.

Multiple lysozymes have been found in at least three species of birds. C. Baker and Manwell (1967) demonstrated that the two lysozymes present in the European quail (*Coturnix*) were due to a genetic polymorphism involving two alleles at a single locus. Similarly, Prager and Wilson (1971) have shown that the three lysozymes found in the egg white of the domestic mallard duck can be explained by a three-allele, one-locus model. However, multiple lysozyme loci also exist in birds, as shown by Arnheim and Steller (1970) in the black swan (*Cygnus atratus*), which produces two antigenically distinct lysozymes. One is seemingly homologous to the chicken enzyme, the other is apparently homologous to that of the goose (*Anser*).

CONALBUMINS

The conalbumins bind two ferric ions (Fe^{+3}) per molecule (Fraenkel-Conrat and Feeney, 1950; Warner and Weber, 1951, 1953), perhaps through coordination with three phenolic (e.g., tyrosyl) oxygen atoms, a bicarbonate ion, and two nitrogen atoms (Windle et al., 1963). The binding of metal apparently leads to a stabilization of the configuration of the molecule. Azari and Feeney (1958, 1961) found that iron-saturated conalbumins were highly resistant to proteolysis, heat denaturation, and attack by organic solvents.

Presumably, conalbumin serves as a source of iron for the developing embryo. By chelating essential metal ions it also has a protective function in inhibiting bacterial growth (Alderton, Ward, and Fevold, 1946; Martin, Jandl, and Finland, 1963; Board, 1970: 257–260) and lipid peroxide formation (Barber, 1961). Feeney and Nagy (1952) showed that the anti-bacterial activity of conalbumin increases as the pH of the egg white increases during incubation.

Although the number of conalbumin bands visible in starch gel patterns varies from one in the kiwi (*Apteryx*) to six in the cassowary (*Casuaris*), the conalbumins are usually seen as a group of three or four bands that migrate either anodally or cathodally depending on the avian group under consideration.

Conalbumins may be referred to as ovotransferrins because of obvious homology to the iron-binding serum transferrins (Williams, 1962, 1968), and, in fact, the synthesis of both proteins is probably controlled by alleles at a single locus (Ogden et al., 1962). Williams suggested that the only difference between transferrin and conalbumin is in the carbohydrate moiety, sialic acid. E. Baker, Shaw and Morgan (1968) demonstrated that most rabbit serum transferrin molecules contain two sialic acid residues; rabbit lactotransferrin has only one. Otherwise, the molecules are identical. For the rock dove (*Columba livia*) Ferguson (MS) showed that treatment of the transferrin with neuraminidase, which removes the sialic acid, resulted in a decrease of electrophoretic mobility so that it became electrophoretically identical to the conalbumin. The electrophoretic heterogeneity and the quantitative relationships of the fractions to one another were unchanged.

In birds of known pedigree, polymorphism in the conalbumins or transferrins has been observed and genetically analyzed in the chicken (*Gallus gallus*) (Lush, 1961; Ogden et al., 1962), ring-necked pheasant (*Phasianus colchicus*) (C. Baker et al., 1966), common (*Columba livia*) and speckled (*C. guinea*) pigeons (Mueller, Smithies, and Irwin, 1962), and red-collared dove (*Streptopelia "humilis" = tranquebarica*). In these instances the conalbumin or transferrin phenotype was shown to be controlled at a single autosomal locus with three co-dominant alleles.

Studies on wild populations have been made by Milne and Robertson (1965), C. Baker and Hanson (1966), Stratil and Valenta (1966), C. Baker (1967), C. Baker and Manwell (1967), Brush (1968, 1970), and Ferguson (MS). Polymorphism of conalbumin and transferrin similar to that found in the laboratory were reported in the following species: domestic goose (*A. anser*), three species of *Branta*, muscovy duck (*Cairina moschata*), black scoter (*Melanitta nigra*), common eider (*Somateria mollissima*), ring-necked pheasant (*Phasianus colchicus*), chukar partridge (*Alectoris graeca*), laughing gull (*Larus atricilla*), black-headed gull (*Larus ridibundus*), wood pigeon (*Columba palumbus*), barbary dove (*Streptopelia risoria*), magpie (*Pica pica*), hooded crow (*Corvus cornix*), red-winged blackbird (*Agelaius phoeniceus*), and Brewer's blackbird (*Euphagus cyanocephalus*).

The fact that such polymorphisms exist and appear to be widespread reduces the importance of the number and mobility of conalbumins for higher category systematics. Still, there is significance in this protein region provided that the interpretation is cautious. The general shape of the electrophoretic pattern produced by the conalbumins in all Galliformes is distinctive, regardless of the differences in the number of components or relative mobilities. The same is true for other groups of birds. The conalbumins may be tightly bunched together as in the Anatidae (figs. 10–12) or rather widely separated as in the Diomedidae (fig. 4). The relative position of the bands may be important, as long as a considerable degree of constancy exists among the species examined. In the Ardeidae (figs. 7–9) and the Accipitridae (figs. 13–15) the position is cathodal. In other groups, such as the swifts (Apodidae), it is well toward the anode (fig. 34). There are also differences between groups in concentrations, relative stability, and other features of conalbumins; these are mentioned under the family accounts.

In two-dimensional starch gel studies on variants of human serum transferrins Connell and Smithies (1959) suggested that the mobility differences among components may be due to charge differences contributed by single amino acid substitutions.

C. Baker (1967) and Stratil (1967a), however, found that the mobilities of the conalbumin fractions in chicken egg white varied with the relative saturation of iron in the sample. They suggested that conalbumin is normally only partially saturated with iron and that the two bands seen in the starch gel pattern correspond to the

metal-free protein and the one-Fe-atom-protein complex. Wenn and Williams (1968) studied this phenomenon by partially saturating conalbumin with ^{59}Fe and separating the components by isoelectric fractionation. They detected unsaturated, half-saturated, and fully saturated (two Fe atoms per molecule) conalbumins and concluded that the binding constants for the two iron atoms are similar.

Greene and Feeney (1968) reduced the disulfide bonds of chicken conalbumin, rabbit serum transferrin, and human serum transferrin, carboxymethylated the resulting sulfhydryls, and attempted to cleave the proteins into smaller subunits by treatment with 8M urea and 6M guanidine hydrochloride. Upon ultracentrifugation they found no evidence of subunits when compared to reduced and carboxymethylated bovine serum albumin and porcine pepsin, and concluded that conalbumin exists as a single polypeptide chain with a molecular weight of about 78,000. They postulated that conalbumin may exist as two roughly identical globular portions joined by a peptide chain.

COMPONENT 18

Present in nearly all electrophoretic patterns is a single band, often streaked in appearance, which migrates slightly toward the anode. It is usually referred to as "Component 18" (Lush, 1961; H. Miller and Feeney, 1964) or ovomacroglobulin (H. Miller and Feeney, 1966; Feeney and Allison, 1969). This protein has a high molecular weight (760,000 to 900,000) and is poorly known. Its persistence in older samples suggests that it may be relatively resistant to denaturation. A general trend is for those groups of birds that are considered more "advanced" to have a C18 of slower mobility. The mobility differences of Components 18 range from that of the ratites, where a usual R_f is 0.25 to 0.30, to that of the New World nine-primaried oscines in which the protein barely migrates anodally from the application point at pH 8.

GLOBULINS

Ahead of the conalbumins in the patterns of many species is a series of small indistinct bands generally referred to as globulins or ovoglobulins without further distinction. They appear to be one of the first groups of proteins to disappear upon incubation or ageing and may not be of great value in interpreting the patterns. Lush's (1964a) reported polymorphisms at Loci II and III of chicken seem to refer, at least in part, to this series. C. Baker and Manwell (1962) also discussed the probable genetic control of variations within a mucin-globulin region of chicken egg white.

OVOMUCOID

Further anodal is the usually large ovomucoid fraction, a glycoprotein of about 28,000 molecular weight, which inhibits the proteolytic and esterase activities of the enzyme trypsin. The chemistry of trypsin-inhibiting proteins has been reviewed by Laskowski and Laskowski (1954), and recently ovomucoid has been considered in detail by Melamed (1966).

The relative electrophoretic mobility of ovomucoid is peculiar. From the molecular sieving properties of starch gel (Smithies, 1962) one would expect that ovomucoid with a molecular weight of about 28,000 would be retarded less than ovalbumin,

which has a molecular weight of about 45,000. Yet in nearly all patterns where ovomucoid appears to be present it migrates cathodal to the ovalbumin. The large carbohydrate moiety that makes up 25% of ovomucoid by weight probably decreases its electrophoretic mobility. Unusual behavior upon dialysis (Craig et al., 1958) and gel filtration (Whitaker, 1963) indicates a larger volume than expected and suggests that the ovomucoid molecule may be highly hydrated.

Feeney et al. (1960) found considerable variation in the amount of ovomucoid among several species of birds, from about 11% of total egg white protein in chicken to 30% in cassowary. Rhodes, Bennett, and Feeney (1960) demonstrated different classes of anti-tryptic activity in ovomucoids of some avian species. Stevens and Feeney (1963) reported that acetylation and carbamylation destroy the trypsin-inhibiting ability of turkey ovomucoid but have no effect on the properties of chicken or pheasant ovomucoid.

The general form, mobility, and concentration of ovomucoid in the starch gel patterns seem to be consistent with natural groupings and are of notable value in the interpretation of patterns. Some species have a number of components in the ovomucoid region. This heterogeneity has been known for some time (Longsworth, Cannan, and MacInnes, 1940; Fredericq and Deutsch, 1949; Bier et al., 1953), but the cause is not yet fully understood. Rhodes, Bennett, and Feeney (1960) found different amounts of sialic acid in the fractions of ovomucoid isolated by ion-exchange chromatography.

OVALBUMIN

The fastest moving major component is ovalbumin, which makes up about 60% of the protein in avian egg white. It consists of a single chain of about 400 amino acid residues and has a molecular weight of approximately 45,000. It will readily be seen from the patterns that this protein displays many characters that can be used to distinguish avian groups. The data on ovalbumin have been reviewed in detail by Neuberger and Marshall (1966) and by Weintraub and Schlamowitz (1970), so only a few points will be discussed here.

Perlmann (1950, 1952, 1955) showed that the three fractions of chicken ovalbumin differ in their phosphate content. The most anodal band contains one phosphate residue per mole of protein, the middle peak two phosphate residues, and the trailing component has no attached phosphate. C. Baker et al. (1966) demonstrated that a similar situation exists in the pheasant *Phasianus colchicus*. Other groups with three ovalbumin bands are the Phalacrocoracidae, Tinamidae, Ardeidae, and probably the Anatidae. Some families (e.g., the Podicipedidae and the Falconidae) show two ovalbumin bands. The cause of the heterogeneity in these latter groups remains unknown. The majority of birds appear to have only one ovalbumin band, at least electrophoretically in starch gel. Sanger and Hocquard (1962) suggested that diphosphorylation takes place by a separate mechanism after the synthesis of the ovalbumin polypeptide chain. They did not, however, find any evidence for the formation of mono-phospho-ovalbumin, which is present in egg white. This implies that the attachment of phosphate may not be static. In other words, species with phosphates attached to the ovalbumin might be expected to show up to three bands upon electrophoresis.

Lush (1961, 1964b), using pedigreed domestic fowl, analyzed genetic polymorphisms at the ovalbumin locus. There appear to be five ovalbumin components that are under the control of two allelic genes. The fact that some heterogeneity of the ovalbumin remained after dephosphorylation with prostatic and intestinal phosphatase

suggests that differences either in the attached carbohydrate or, more likely, in the amino acid sequence of some of the components may be responsible for the variation. Using two-dimensional chromatography and electrophoresis Wiseman and Fothergill (1966) distinguished two variants of chicken ovalbumin that differed by a single chymotryptic peptide and, presumably, by a single amino acid.

C. Baker (1965) found polymorphism in the ovalbumins of the pheasant genus *Chrysolophus*. Although the number of individuals examined was too small to permit conclusive analysis, the situation seems to be similar to that reported by Lush. Much of the variation in the ovalbumins of phasianids in general (figs. 16–18) probably is attributable to this phenomenon (see further comments under accounts of the Galiformes). In other groups with multiple ovalbumins the situation seems to be different. Members of the Phalacrocoracidae, for example, show little variation in the mobility, number, or concentration of their ovalbumins (figs. 6, 7), so that it is difficult to establish polymorphisms in many groups on the basis of this study. Those species with a single ovalbumin also are not seen to vary. If amino acid differences are involved in the polymorphism, they may not cause changes in charge or shape and hence go unnoticed by electrophoresis.

Some research on ovalbumin has centered on the nature of the carbohydrate moiety (see review by Gottschalk and Graham, 1966). It is now fairly well established that the carbohydrate is a branched structure consisting of approximately three N-acetyl-glucosamine and five or six mannose residues linked to aspartic acid in the polypeptide chain as 2-acetamido-1-(L- β -aspartamido)-1, 2-dideoxy- β -D-glucose (see, e.g., Clamp and Hough, 1965; R. Marshall and Neuberger, 1964; Montgomery, Lee, and Wu, 1965). Weintraub and Schlamowitz (1970) have reviewed and extended the study of the carbohydrate moiety of the ovalbumins of chicken, turkey and duck. They found small differences among the three species, with chicken and duck being most alike in total carbohydrate content.

Little is known about the amino acid sequence of ovalbumin. For chicken ovalbumin Narita and Ishii (1962) determined an N-terminal sequence of AcGly-Ser-Gly-Ileu-Ala. . . . Niu and Fraenkel-Conrat (1955) demonstrated a C-terminal sequence of . . . Val-Ser-Pro. The primary structure of the peptide to which the carbohydrate moiety is attached (Lee and Montgomery, 1962) and of peptides containing cystine (Anfinsen and Redfield, 1956) also have been established, but the positions of these peptides along the chain are not known.

PREALBUMINS

In some species a "prealbumin" is found migrating farthest anodally, in front of the ovalbumin. This probably represents the riboflavin-binding protein discovered by Rhodes, Bennett, and Feeney (1959) and reported by C. Baker and Manwell (1962) as migrating ahead of ovalbumin in starch gel patterns of chicken egg white. C. Baker et al. (1966) found three prealbumins in *Phasianus colchicus*. They identified the most basic of these as the riboflavin-apoprotein complex. There are apparently two prealbumins in *Chrysolophus* (C. Baker, 1965). Two also occur in the chicken (Lush, 1961; C. Baker and Manwell, 1962). Four have been found in the Japanese quail (*Coturnix coturnix*) (C. Baker and Manwell, 1967) and up to six in the silver pheasant (*Lophura nycthemera*) (C. Baker, 1968).

There is as yet no clear evidence to indicate that prealbumins in non-phasianids are necessarily homologous proteins. It should be pointed out that in their analyses Baker and co-workers employed different buffer systems (see especially C. Baker, 1964, for details) to resolve the apparently acidic and low molecular weight pre-

albumins. The lack of prealbumins in our patterns of *Phasianus* and *Chrysolophus* (figs. 16, 17) should not be interpreted as a contradiction of data. Rather, the prealbumins are probably masked by the ovalbumin in our starch gels.

MUCINS

The mucins do not migrate through the starch gel and frequently may be observed as precipitated, stained protein at the application point. Such behavior probably results from the fibrous structure postulated for ovomucin (Brooks and Hale, 1961).

MATERIALS AND METHODS

The rationale for using protein molecular characteristics as indices to genetic relationships, the electrophoretic techniques employed in this study, and the criteria followed in the interpretation of the starch gel patterns have been described by Sibley (1970: 9-22). Additional discussions and descriptions of procedures are to be found in Sibley (1960, 1962, 1967), Sibley, Corbin and Ahlquist (1968), and Sibley, Corbin and Haavie (1969).

About half of the more than 12,000 specimens of egg white used in these studies is from non-passerine birds. This paper is based upon material from 816 species representing 88 of the 95 non-passerine families recognized by Wetmore (1960). Those groups not represented are the Balaenicipitidae, Mesitornithidae, Pedionomidae, Dromadidae, Leptosomatidae, Brachypteraciidae, and Ramphastidae.

The presentation of material in this paper follows the systematic sequence of Wetmore (1960) with some regroupings for clarity in presenting the data and some representing proposals for changes in classification. The family names are those used by Wetmore. The nomenclature for genera and species is mainly that of Peters (1931-48), but for some groups where a later revision has been made, we have followed it and cited the source at the beginning of the list of species examined. For each group there is a fraction, e.g., 1/18, indicating the number of species for which egg white has been studied and the number of species in the group. The latter figure is that given by Mayr and Amadon (1951), except where a later revision has been made.

The historical review usually follows a chronological order. We have attempted to provide the reader with the principal conclusions of various authors and to indicate the bases for them. The literature search has not been exhaustive, but we have sampled the range of previous opinions concerning the relationships of each group. For the most part we have not attempted to evaluate the bases for taxonomic opinions because to do so would have produced a much lengthier manuscript and because the conflicting opinions themselves, often based on the same evidence, demonstrate the hazards in interpreting the taxonomic significance of various characters. Following the historical account we have summarized the trends in thought of systematists regarding each group. This is followed by a consideration of the egg white protein evidence in light of the historical background.

The figures have been assembled to provide patterns for as many of the available species as possible. When a pattern from a species listed as being studied is not included in the plates, it should be taken to mean that the pattern of this species is essentially like those of its congeners and that a pattern of optimum quality for reproduction was not available. In a few instances involving unusual species we have included a poor pattern when it was the only one available.

ORDER SPHENISCIFORMES

Family Spheniscidae, Penguins

Wetmore, 1960

INTRODUCTION

The principal questions concerning the relationships of the penguins are: (1) Did the penguins have flying ancestors? (2) To which group of living birds are the penguins most closely allied? A review of the history of the opinions about these questions reveals considerable diversity and indicates the sources of the classifications currently in use.

HISTORICAL REVIEW OF THE CLASSIFICATION

Nitzsch (1840) included the penguins in his Pygopodes along with the loons, grebes, and alcids because it was apparent to him that the characteristic pterylosis of penguins is an adaptation to an aquatic environment rather than evidence of a completely independent origin.

G. Gray (1849) placed the penguins in his Anseres, which contained most of the swimming birds. The position of the penguins in Gray's classification is interesting—he placed them between the Uridae (= *Uria*) and the Alcidae (the other auks and puffins).

Huxley (1867: 430) observed: "In the Gulls, the Divers, the Grebes, the Auks, and the Penguins, the bones which form the roof of the mouth have the same general arrangement and form as in the Plovers. But they are devoid of basipterygoid processes; and in the Penguins the pterygoids become much flattened above downwards." Huxley treated the penguins as a separate group, the Spheniscomorphae. He placed them among the schizognathous birds and was impressed by their similarities to the alcids, particularly to the great auk (*Pinguinus impennis*).

The pelvic muscle formula of penguins is ABX+ (Garrod, 1873d; 1874a), a condition shared by most Procellariiformes as well as by a number of other birds. Garrod included penguins in his cohort Anseres, along with the Anatidae, Colymbidae (= Gaviidae), and Podicipidae (= Podicipedidae).

From an osteological study Gervais and Alix (1877) thought that penguins were related to some group of swimming birds but did not speculate further. P. Sclater (1880) gave the penguins ordinal rank as the Impennes between his Pygopodes (= Gaviidae, Podicipedidae, and Alcidae) and Crypturi (= Tinamidae). Reichenow (1882) placed them in his order Urinatores along with loons, grebes, and auks.

Following a detailed anatomical study of penguins Watson (1883: 232) concluded that "they form the surviving members of a group which had early diverged from the primitive avian stem, but that at the time when the separation took place the members of that stem had so far diverged from the primitive ornithoscelidian form as to be possessed of anterior extremities, which instead of forming organs of terrestrial, had become transformed into organs adapted to aerial progression, in other words, into true wings." In the absence of a more complete fossil record, however, Watson would not speculate about the closest living relatives of the penguins. He noted only that they seem close to the "Palmipedes," i.e., the web-footed birds.

Stejneger (1885) emphasized the differences between penguins and other birds and erected a superorder Impennes for them. Menzbier (1887) also separated the penguins as the Eupodornithes, one of his four divisions of the class Aves. He suggested that penguins may have had a reptilian ancestry separate from that of other birds.

The penguins are most closely allied to the Procellariiformes, according to Fürbringer (1888). He thought that they were not descended from any living procellariiform birds but that the two groups shared the same ancestry.

The patterns of intestinal convolutions in the penguins, Gadow noted (1889: 311-12),

possess undeniable characters in common with the Pygopodes, Steganopodes (= Pelecaniformes), and Tubinares (= Procellariiformes); they are on the whole orthocoelous, but the extreme length of their gut thrown into numerous straight and oblique, or quite irregular convolutions, renders comparison very difficult. They have probably branched off very early from the main orthocoelous stock in the Antarctic region, and thus have had time to assume, through intense specialization, those pseudo primitive characters in their whole organization which now separate the few surviving forms from the rest of the birds.

After careful consideration of many lines of evidence Gadow (1893) also concluded that the penguins were closest to the Procellariiformes. He felt that a more distant relationship to the loons and grebes was possible.

Seebohm expressed several opinions regarding the relationships of the penguins. In his 1888b paper he listed their osteological peculiarities and seemed convinced that their nearest allies are the loons and grebes. In his 1890a classification the penguins appear as the order Impennes between the order Tubinares and the Gaviae (= gulls and terns) of his order Gallo-Grallae. In 1895, other than admitting that penguins had been derived from flying birds, he gave no opinion as to their nearest relatives. "To give them time to metamorphose their wing into paddles so completely as they have done, it must be assumed that their isolation occurred at a very early date, sufficiently early to warrant us in regarding the Penguins as the survivors of a group of birds whose isolation dates back far enough to entitle them to hold rank as a subclass" (p. 9).

Sharpe (1891) retained ordinal status for the penguins, placing them between

his Pygopodes (loons) and Tubinares. In his diagram of proposed relationships the penguins appear somewhat closer to the loons (as well as the grebes) than to the Procellariiformes.

Of the penguins Newton (1893-96: Intro, p. 111) wrote: "There is perhaps scarcely a feather or a bone which is not diagnostic, and nearly every character hitherto observed points to a low morphological rank. The title of an Order can scarcely be refused to the *Impennes*." Beddard (1898a) was equivocal concerning the affinities of the penguins. Without comment he placed them between the Hesperornithes (= *Hesperornis*) and the Steganopodes (= Pelecaniformes). On the other hand, Pycraft (1898c) found penguins to be osteologically most like the Procellariiformes, with a lesser degree of resemblance to the loons and grebes.

Ameghino (1905), who described many fossil birds from Patagonia, thought that the ancestors of modern penguins progressed through a flightless terrestrial stage before becoming aquatic. He also concluded that the early Tertiary penguins were more specialized than Recent forms, particularly with regard to their relatively longer and more fused tarsometatarsi, and therefore could not be ancestral to modern penguins.

Wiman (1905) thought that early Tertiary penguins were osteologically more like other carinate birds than are modern penguins. He noted some points of similarity to the Procellariidae but drew no taxonomic conclusions from his observations.

With reference to the feathers of penguins, Chandler (1916: 298) concluded that "the uniform distribution of feathers, the absence of specialized remiges and of under wing coverts with a reversed position, and the simple structure of both their pennaceous and their downy barbules, all point to their low systematic position." He believed that penguins were derived from extinct, toothed, aquatic birds.

E. Stresemann (1927-34) concurred with Fürbringer and Gadow that the penguins are most closely related to the Procellariiformes. Wetmore (1930) and Peters (1931) ranked the penguins as an order between the ratites and the loons and grebes. However, following Lowe (see below), Wetmore (1934, 1940, 1951) revised his opinion and elevated the penguins to superordinal rank at the base of his linear sequence.

A detailed analysis of the vertebral column and hind limb in penguins by Virchow (1931) supported the hypothesis that the modifications observed in these structures arose primarily for underwater propulsion. Movement on land by walking upright or by "tobogganing" on snow or ice using both wings and feet is correlated with and modified by adaptations for swimming. Another osteological study, that of Boas (1933), supported a penguin-procellariiform alliance.

Several lines of evidence led Lowe (1933a, 1939a) to assert that penguins and other carinate birds originated from two separate stocks. Furthermore, he maintained that the ancestors of penguins never flew. His conclusions were:

- 1) The lack of apteria, the extreme proliferation of feathers over the body and wings, and the failure of the remiges to differentiate from coverts are primitive features. Perhaps each feather corresponds to a scale of the ancestral reptile. In *Aptenodytes* the first two rows of feathers implanted above the rear edge of the wing are probably homologous to the median and greater underwing coverts. The third dorsal row of feathers are actually the remiges. This is a primitive feature because it is the embryonic condition of carinate flying birds, as shown by Wray (1887). In adults of carinate birds, of course, the remiges grow out a considerable length over the ventral coverts.

- 2) Since the structure of the wing bones in early penguin embryos is like that of the adult and there is no approach to the embryonic carinate condition, the penguins must have had a distinct ancestry.

3) Miocene penguins are similar to modern forms with no suggestion of being intermediate to a presumed flying ancestor, thus proving that penguins did not have flying ancestors.

4) "The tarso-metatarsus of Penguins . . . is absolutely unique in the class Aves; a similar modification is conspicuous in the bipedal Dinosaurs (*Ceratosaurus* Upper Jurassic), and it may be that the physiological factors which led to the same morphological results in the two categories of animals concerned may imply an inheritance from a common ancestor, and not merely and only the convergent effects of similar habits. Thus the tendency to stand really upright may be inherited from a common ancestor, as may be the morphological and physiological details by which that habit finds expression" (p. 513).

5) The arrangement of certain muscles (rectus abdominis, pars abdominalis of the pectoralis major), the lack of pneumaticity in the bones, and other characters are primitive.

With regard to Lowe's first point (above) we maintain that his own evidence negates his hypothesis of avian polyphyly. It seems unlikely that convergence would produce identical feather arrangements in both embryo and adult birds derived from separate reptilian lineages.

Gregory (1935) pointed out that the characters used by Lowe in arguing for a separate reptilian ancestry for the penguins could be better understood as adaptations to an aquatic habitat. He emphasized the similarity of the wing of penguins to that of flying birds, and added (p. 10): "It is in the entire pectoral girdle, however, that the penguins retain the most convincing evidence of derivation from completely flying carinate birds. Here are essentially the same outstandingly avian characters of the blade-like scapula, the well developed furcula, the elongate coracoids, the foramen triosseum, the well developed carina and the enormous sternum. With all this the penguins merely fly under water instead of in the air." Lowe's arguments from the fossil record were also unacceptable to Gregory, who noted that all avian orders are distinguishable by the early Tertiary, and therefore that it is unwise to claim that the similarity of the Miocene or Eocene penguins to modern forms proves great antiquity or suggests an evolutionary history distinct from that of other birds.

Murphy (1935: 16) disagreed with Lowe's interpretations of the pterylographic evidence. "The feather arrangement along the hind edge of the wing is . . . persistently embryonic, but it does not follow that this is phylogenetically primitive. On the contrary, the condition is one that would almost necessarily be restored with the reduction of large flight-quills to the size of undifferentiated coverts." The reduction in size and increase in number of penguin remiges clearly is an adaptation for under-water propulsion.

From another point of view—a consideration of life histories and general adaptation—Murphy and Harper (1921) and Murphy (1936: 776-77) were impressed with the similarities between the diving petrels (*Pelecanoides*) and the penguins. This was not meant to imply a close relationship between the two groups, but to show how a bird with characters like those of the procellariiforms could have been an intermediate stage in the evolution of penguins.

Simpson (1946) reviewed the fossil penguins and speculated on the origin of the group. He criticized Lowe (1933a, 1939), charging that his interpretation of the fossil record suffered from polemics. "The species singled out by Lowe to represent Miocene penguin morphology seem to me to be the most specialized and aberrant members of the group . . ." (p. 43). Of the affinities of penguins Simpson stated (p. 84):

Excepting only the wing and the tarsometatarsus, the recent penguin skeleton

is remarkably like that of many flying carinates and particularly of the Procellariiformes, as has been repeatedly noticed and can be confirmed by comparison of the skeletons of almost any genera of the two groups. If this similarity were a coincidence or due wholly to convergence, the Miocene penguins might be no less similar to the Procellariiformes but surely would not be expected to be more similar. The fact that they are more similar, even though in slight degree, is good supporting evidence that their remote ancestry was indeed like, if not identical with, that of the Procellariiformes.

It seemed most reasonable to Simpson that the ancestors of penguins were aerial oceanic birds which, as an intermediate stage, adopted submarine as well as aerial flight. In the final stage, represented by penguins, exclusive submarine flight replaced aerial flight.

Since the publication of Simpson's paper, additional fossil penguins have been described (Marples, 1952; Simpson, 1957, 1959, 1965, 1970), particularly from Australia and New Zealand. Although some of these forms extend the age of the Spheniscidae back to the Eocene, they do not shed any new light on the origin of penguins or the ancestry of extant species.

Howard (1950) followed Simpson's conclusions, as did Mayr and Amadon (1951: 4-5), who stated that the "penguins are related to the petrels and less closely to the Steganopodes."

Crompton (1953) studied the development of the chondrocranium in *Spheniscus demersus* and found that its structure is typically avian. He agreed that the Procellariiformes are the closest relatives of the penguins.

Penguins have a Type A-1 carotid artery pattern, a Type A coracoid artery, and Type 1 thoracic artery (Glenny, 1944, 1947, 1955). This agrees with the condition found in the Gaviidae, nearly all Procellariiformes, and many Charadriiformes, among others.

Verheyen (1958e, 1961) maintained that there was no conclusive evidence indicating that penguins were derived from flying ancestors. He considered them to be distantly allied to the kiwis on one hand and to the shearwaters and alcids on the other. In his final classification Verheyen (1961b) placed the penguins as an order beside the Procellariiformes in his superorder Hygrornithes.

In spite of the evidence for a penguin-procellariiform relationship, Wetmore (1960: 4) noted:

The question of the weight to be given the peculiarities of uniform pterylosis, extreme specialization of the wing as a flipper for submarine progression, and incomplete fusion in the metatarsal elements, as well as such other details as erect posture in standing and walking and the anatomical adjustments involved, found in the penguins, is one that has merited careful review. It seems reasonable after this examination to retain the Impennes as a superorder, at least until we have further evidence through fossils as to their line of evolution.

Storer (1960a: 61) agreed with Wetmore. "These differences between penguins and other birds are sufficient to merit the erection of a superorder for the penguins, yet phylogenetic evidence could justify placing these birds next to the petrels."

The paper electrophoretic patterns of the egg white proteins of *Spheniscus demersus* neither supported nor denied a relationship with the Procellariiformes and did not suggest an alliance to any other group (Sibley, 1960). While aware that some changes in the proteins probably occurred since the divergence of the line leading to

penguins, Sibley deferred a final decision until additional penguin material could be studied.

Kinsky, in describing the young of the little blue penguin (*Eudyptula minor*), noted that the "nostrils of small chicks are tubular, with large, nearly round apertures (Fig. 14). The tubes start to recede during the sixth week of age and the openings start flattening. This change is completed within one week, and at the age of 43 days the slit-like nostrils of the adult bird are formed" (1960: 169). It would be interesting to ascertain if this structure is homologous to the tubular nostrils of adults and young of the Procellariiformes.

Meister's (1962) histological study of the long bones of the penguins disclosed differences from other birds in the general structure of the bone, the disposition of the marrow, and the arrangement of the Haversian system. These characters point to the distinctiveness of penguins but reveal little about their affinities. These features may also be adaptive responses to underwater swimming.

In his paper on cranial morphology and kinesis Simonetta (1963) observed that penguins are most similar to the grebes and loons. Such similarities are as likely to be due to convergence as to common ancestry.

Gysels (1964) examined the lenticular proteins of the penguin *Spheniscus humboldti* but was unable to find evidence of close relationship to the Procellariiformes. He suggested, however, that the closest relative of the penguins is the common murre (*Uria aalge*) but not the other Alcidae. This opinion was based on the alleged similarity of the immunoelectrophoretic patterns and the lack of glycogen in the lenses of *Spheniscus* and *Uria*, a "primitive" character according to Gysels. Glycogen was present in the lenses of *Fulmarus glacialis*, the only procellariiform studied, and of Charadriiformes other than *Uria*.

The fine structure of the egg shells of several penguins was described by Tyler (1965). A plot of total shell nitrogen against shell thickness showed some separation of the genera and species. One main group consisted of *Pygoscelis adeliae*, *P. antarctica*, *Eudyptes crestatus*, *E. chrysolophus*, *Megadyptes antipodes*, *Eudyptula minor*, *Spheniscus humboldti*, and *S. magellanicus*. A second group included only the shells of *Pygoscelis papua*, with one exception. *Aptenodytes forsteri* and *A. patagonica* formed a third group.

The egg white protein studies of the Adélie penguin (*Pygoscelis adeliae*) by Feeney et al. (1966) determined the properties of the various proteins, and compared the penguin egg white electrophoretically and immunoelectrophoretically with that of several other species of birds. Anti-penguin egg white antisera showed strong cross-reactivity with egg white of the pink-footed shearwater (*Puffinus creatopus*), Laysan albatross (*Diomedea immutabilis*), western grebe (*Aechmophorus occidentalis*), and mallard duck (*Anas platyrhynchos*). Cross-reactivity between the anti-penguin egg white antiserum and egg white of the chicken (*G. gallus*) and cassowary (*C. casuaris*) was noted only for the ovomacroglobulin (= Component 18), thus suggesting to the authors that the penguins are not closely allied to the ratites.

Allison and Feeney (1968) reported on the serum proteins of three penguins, the Adélie, emperor (*Aptenodytes forsteri*), and Humboldt (*Spheniscus humboldti*). The serum transferrins of the Adélie and emperor were nearly identical to one another and showed four or five bands in starch gel. The Humboldt had two transferrin bands of slower mobility than those of the other two penguins. The serum albumins and transferrins of the three penguins were more alkaline than those of the chicken. Essentially the same information on the egg white and blood proteins of the Adélie penguin was presented by Feeney et al. (1968).

Margoliash and his associates (Chan and Margoliash, 1966; Chan et al., 1963; Chan, Tulloss, and Margoliash in McLaughlin, 1969; Margoliash, Needleman, and

Stewart, 1963) have determined the amino acid sequences for the cytochromes *c* of the chicken (*G. gallus*), turkey (*Meleagris gallopavo*), mallard duck (*Anas platyrhynchos*), pigeon (*Columba livia*), and king penguin (*Aptenodytes patagonica*). The amino acid sequence of chicken cytochrome *c* is identical to that of the turkey and differs from the cytochrome *c* of the penguin by two amino acid substitutions, from that of the mallard by three substitutions, and from that of the pigeon by four substitutions. Each of these substitutions can be accounted for by single nucleotide base-pair changes (see Dayhoff 1969: D-195). Although it is unwise to propose relationships from this limited information, the data do suggest that the penguins may be more closely allied to certain other carinate birds than some carinates are to one another. The cytochrome *c* of the chicken, for example, is more similar to that of the penguin than it is to those of either the duck or pigeon.

SUMMARY

Three theories of penguin evolution have been presented by various authors:

- 1) The ancestors of penguins were terrestrial, non-volant birds that secondarily became aquatic.
- 2) The ancestors of penguins were volant, terrestrial birds that subsequently lost the ability to fly and later became aquatic.
- 3) The ancestors of penguins were volant oceanic birds that increasingly used their wings for propulsion underwater and finally became exclusively submarine fliers.

Of these, the third seems to us to be the most plausible and seems to be supported by the majority of the available evidence. There is a consensus that the Procellariiformes are the nearest living relatives of the penguins, but this should not be regarded as proof of such a relationship. In order of decreasing frequency of proposal, the Gaviiformes and Podicipediformes, the Pelecaniformes, and the Apterygiformes have also been thought to be the nearest allies of the penguins.

THE EGG WHITE PROTEIN EVIDENCE

ORDER SPHENISCIFORMES

FAMILY SPHENISCIDAE, Penguins. 10/16, fig. 2.

Species examined: *Aptenodytes forsteri*; *Pygoscelis adeliae*, *antarctica*, *papua*; *Eudyptes chrysolophus*, *crestatus*; *Spheniscus demersus*, *humboldti*; *Eudyptula minor*, *albosignata*.

The starch gel pattern of penguin egg white is simple. There are no cathodal components. Component 18 is strongly defined and the conalbumins migrate near it. The latter occur between the application slot and Component 18 in *Spheniscus humboldti*, on both the anodal or cathodal sides of Component 18 in *Pygoscelis papua*, and entirely anodal to C18 in *Eudyptes chrysolophus*. In slightly denatured samples the conalbumins appear as a smear anodal to Component 18. The next major protein is ovomucoid, which appears as a single broad band. (Some minor fractions may be seen between the conalbumins and the ovomucoid in some species.) Immediately anodal to the ovomucoid is ovalbumin, which is less concentrated than the ovomucoid. There is some "tailing" in the ovalbumin region in the patterns of *Eudyptes chrysolophus* and *Pygoscelis papua*, suggesting that two bands may be present. A prealbumin appears in the patterns of *Spheniscus*.

The penguins are members of an assemblage of aquatic birds with similar starch gel egg white patterns. In this group we include the Gaviidae, Procellariiformes, Charadriiformes, and, possibly, the Pelecanidae and Fregatidae. The patterns of these birds contain a small number of components, and homologous proteins have similar mobilities. The arrangement and shape of the bands are simple, but each group subtly differs from the others. Do the small visible differences among the patterns indicate rather large changes in the primary structures of the proteins involved? Or are the similarities indicative of fairly close relationships among the birds themselves? The interpretation of these patterns is difficult and we have been cautious in ascribing too much importance to them. We treat this matter in detail in the accounts of each of the above named groups.

The mobility of Component 18 in the starch gel pattern of the penguins is like that of many Procellariiformes. The conalbumins are variable and those of a given species of penguin can be found to match in number and mobility those of some procellariiform species. The ovomucoid of penguins has a greater anodal mobility and usually a higher concentration than that of the Procellariiformes. The ovalbumins of both groups have the same mobility, but in some penguins (e.g., *Pygoscelis papua* and *Eudyptes chrysolophus*) the ovalbumin is less concentrated. When compared to the patterns of the charadriiforms and loons the ovalbumin of penguins is seen to have a slower anodal mobility and the ovomucoid a faster anodal mobility.

The patterns of the grebes differ from those of the penguins in three ways. The ovomucoid of grebes has a greater anodal mobility than that of penguins, the conalbumins are characteristically arranged anodal to Component 18, and the ovalbumin band of grebes is double.

CONCLUSIONS

Although several groups of aquatic birds have similar egg white patterns, we conclude that the penguin patterns are more like those of the Procellariiformes than those of any other group. We favor a classification indicating such an alliance, even though the degree of relationship is still uncertain. The egg white protein evidence does not suggest which members of the Procellariiformes may be closest to the penguins or which penguin genera are closest to each other.

THE RATITES, KIWIS AND TINAMOUS

Order Struthioniformes
Family Struthionidae, Ostriches
Order Rheiformes
Family Rheidae, Rheas
Order Casuariiformes
Family Casuariidae, Cassowaries
Family Dromiceidae, Emus
Order Apterygiformes
Family Apterygidae, Kiwis
Order Tinamiformes
Family Tinamidae, Tinamous

Wetmore, 1960

INTRODUCTION

We will discuss the tinamous and kiwis with the large ratites because much of the literature deals with all three groups. Two questions confront us regarding the evolution of these birds: (1) Have the flightless ratites been derived from flying ancestors? (2) What are the relationships of the large ratites to one another, to the kiwis and tinamous, and to other birds?

HISTORICAL REVIEW OF THE CLASSIFICATION

Merrem (1813) was the first to place the large ratites in a group separate from other birds because they lacked a keel on the sternum. Lesson (1831) concurred, placing the large ratites and kiwis in the major division "Oiseaux Anormaux," as opposed to the "Oiseaux Normaux," which contained all other birds. He recognized two "families," the Nullipennes for *Apteryx* and the Brevipennes for the rest. In his system the tinamous are put with the gallinaceous birds.

It was clear to Darwin (1859: 106, 226) that the flightless ratite birds had evolved from flying ancestors through "disuse" of their wings and increasing use of their hind limbs. Owen (1866, v.2: 12) was not a strict believer in natural selection, but characterized the "cursorial" birds by the "arrested development of the wings unfitting them for flight." Although he grouped all flightless birds together, he recognized that they were not all closely related. For example, he thought that the ostrich was allied to the bustards (Otididae) and that *Apteryx* and *Dinornis* were closest to megapodes (Megapodiidae). Owen (see review, 1879) also contributed extensively to our knowledge of the extinct Dinornithidae.

Huxley (1867) described the dromaeognathous palate which the large ratites, kiwis and tinamous possess, but he emphasized skeletal differences and made five groups within the Ratitae, one of his three major orders of birds. He placed the tinamous in the order Carinatae but near the large ratites and the kiwis.

Mivart (1877), who studied the axial skeleton, treated the large ratites and kiwis as a single family without speculating on their nearest relatives. In a dendrogram he placed *Rhea* and *Struthio* together, *Dromaius* with *Casuarius*, and *Apteryx* with *Dinornis*.

An osteological study convinced Seebohm (1888b) that the tinamous were allied most closely to gallinaceous birds. He put them in a suborder, Crypturi, next to his suborders Gallinae and Pterocletes (sandgrouse).

Gadow (1889) found the ratites to be heterogeneous on the basis of their intestinal convolutions. The ratites agree only in having the second intestinal loop right-handed and the third left-handed. This feature occurs also in the tinamous, gallinaceous birds, *Opisthocomus*, and the Cuculidae.

From a study of the pterylosis of the wing, Wray concluded that "the wings of the Ratitae are of the same general plan as those of the Carinatae, presenting a modification of a more generalized type, which correlates with their bony structure" (1887: 350). In another study of pterylosis, Goodchild commented that "the wing style of the tinamous (Crypturi) differs in no essential respect . . . from that of the Gallinae" (1891: 324).

Although many writers after Huxley treated the ratites as a single group, Fürbringer (1888, 1902) argued that the similarity of characters among the ratites, including the palatal structure, was due to convergence and that each main group originated independently. Gadow (1893), however, furnished additional evidence for the homogeneity of these birds, and Newton attacked Fürbringer's argument for a multiple origin of the ratites, calling it "hardly convincing" and contending that "the characters possessed by all of them in common . . . point indubitably to a single or common descent" (1893-96: Intro. p. 108).

Beddard (1898a) placed the large ratites and *Apteryx* in his order Struthioness next to the order Tinami. He found many points of agreement between the Struthioness and Tinami and some between the tinamous and the galliforms. Beddard disagreed with Fürbringer's wide separation of the various groups and cited several characters, including the palate, which he felt demonstrated a common ancestry, at least for the large ratites and the kiwis. He commented (p. 494) that "there is no doubt that the various types of struthioness birds do require separating into at least six families; but the likenesses among them appear to me to forbid any wider separation."

Following a study of the osteology, myology, pterylography and reproductive system of ratites, Pycraft (1900) included all of them in his superorder Palaeognathae. In his opinion, the Palaeognathae are polyphyletic with *Rhea*, the tinamous, *Aepyornis*, and *Dinornis* composing one group and *Dromaius* and *Casuarius* close to each

other with *Struthio* not distantly allied. *Apteryx* stands apart but closest to the Dinornithidae.

H. Clark (1901b) proposed a classification of birds based on pterylography. He made a single order of the ratites and placed the tinamous among the gallinaceous birds.

From studies of skeletal development in the ostrich, Broom (1906, 1913) concluded that birds as a class had evolved from a group ancestral to the theropod dinosaurs, namely, the pseudosuchian reptiles.

The patterns of the intestinal convolutions were interpreted by Mitchell (1896a: 141) to indicate that *Rhea* is intermediate between *Struthio* and *Dromaius*. Mitchell (1901a: 216) found the convolutional pattern of the tinamous to be unlike that of the ratites and galliforms but similar to that of the bustards (Otididae).

Beddard (1910) disagreed almost completely with Mitchell. He found that the large ratites differ considerably from one another in their intestinal coils but that there are similarities between *Rhea* and the tinamous. Beddard thought that *Apteryx* and the tinamous are similar to gallinaceous birds in these characters, in spite of dietary differences, particularly between *Apteryx* and the Galliformes.

L. Harrison (1916a,b) believed that the Mallophaga provided evidence that *Apteryx* is related to the rails and have nothing in common with the other ratites. "Of the latter, the Ostriches and Rheas would seem to have certainly originated from a common ancestral stock, from which I believe the *Emeus* [*sic*] also to have been derived, though the evidence here is not quite so convincing" (1916b: 259-60).

In a detailed account of feather structure Chandler (1916) argued that the large ratites and the kiwis, and especially *Struthio*, were not derived from flying ancestors. He cited the following as primitive characters: (1) the absence of plumules, filoplumes, and aftershafts; (2) the virtual absence of apteria; (3) the similarity of teleoptiles to neossoptiles; and (4) the structure of the barbules. He suggested that *Struthio* and *Rhea* form one group, the Casuariiformes and *Apteryx* another.

In Chandler's opinion, the distinctive, well-developed, interlocking mechanism of the barbs of tinamous feathers was sufficient to disprove a relationship to the ratites, yet it is clear that the lack of this character in ratites is correlated with their flightlessness. He also found the structure of the down in the tinamous *Calopezus* (= *Eudromia*) and *Nothura* to be the same as in the Galliformes. This he interpreted as indicating "unmistakable relationship" (p. 342).

E. Stresemann (1927-34) followed Fürbringer by placing each of the large ratite groups, the tinamous and the kiwis in separate orders. The similarities between the tinamous and the Galliformes were attributed to convergence.

Brock (1937) studied the cartilaginous skull of the embryo ostrich and found no evidence to indicate that the ostrich is an offshoot of the avian line before the evolution of flight. Steiner (1936) and Lutz (1942) observed that the structure of the emu embryo closely resembles that of carinate embryos. The hallux is opposed to the other digits, as in carinate birds. Because the first digit is lost in the adult, Lutz postulated that the ancestors of emus either lived in trees or had a greater development of the hind toe.

In a series of papers (1928, 1930, 1935, 1942, 1944) Lowe proposed and defended the idea that the ratites and coelurosaurian reptiles like *Struthiomimus* and *Ornitholestes* had a common ancestry. In his view the ratites descended from birds that had never acquired the power of flight. Thus he regarded *Archaeopteryx* as an early offshot in reptilian radiation, not important in the evolution of birds. The main points in his argument for a common ancestry are as follows. (The use of the word "primitive" is Lowe's).

1) In all ratites: the primitiveness of the dromaeognathous palate, the musculature, and the plumage structure.

2) In *Struthio*: (a) the absence of the rudimentary clavicle in the embryo; (b) the persistence of skull sutures; (c) the obtuse angle between coracoid and scapula; (d) the similarity of the manus to that of *Ornitholestes*.

Both Gregory (1935) and Murphy (1935) disagreed with Lowe's interpretations and in careful critiques refuted the arguments of his earlier papers on ratites. However, Friant (1945a, b; 1946, 1959), who also studied osteology, agreed with Lowe's conclusions regarding the primitiveness of the ratites.

The ratites, although related to one another, had an origin separate from that of other birds, according to Oliver (1945, 1949). He believed that tinamous are ratite birds that had achieved flight. Steiner (1949, 1956, 1958) demonstrated the evolution of ratites from carinate birds, using evidence from the arrangement and structure of ratite wing bones and the distribution of primaries, secondaries and their coverts.

McDowell (1948) considered the palaeognathous palate (= dromaeognathous of Huxley) to be variable and impossible to define. He distinguished four morphological types of this palate, and recognized four corresponding orders: Tinamiformes (for Tinamidae and Rheidae), Apterygiformes (for Apterygidae, Dinornithidae, and possibly Aepyornithidae), Casuariiformes, and Struthioniformes.

Howard (1950) reviewed the fossil evidence on the ratite problem and found it inconclusive in assessing their relationships. Berlioz (1950) accorded the several ratite taxa only familial status in his order Struthioniformes, while Mayr and Amadon (1951:4) noted that "the present consensus is that the main groups of these birds are of independent origin."

Rhea and *Struthio* are parasitized by Mallophaga of the same genus (*Struthioli-peurus*), which is found on no other birds (Rothschild and Clay, 1952: 145). They also share the same species of cestode (*Houttuynia struthiocameli*), which is not found in other birds, and two species of Acarina (*Paralges pachycnemis* and *Pterolichus bicaudatus*). Although the similarities of parasites indicated to these authors a common ancestry for the ostrich and rheas, von Keler (1957) was not convinced of the close relationship of the feather lice and suggested that their similarities might be due to convergence since the hosts have similar feather structures. Clay (1950, 1957) found that the Mallophaga of tinamous resemble those of gallinaceous birds.

The structure of the ostrich chondrocranium does not differ in any essential detail from that of carinate birds (Frank, 1954). After a study of the ontogeny of cranial bones and nerves of *Struthio*, Webb concluded that the Dromaeognathae are not primitive but "rather they are a neotenic offshoot of some ancestral bird or birds" (1957: 145). He derived the palatal structures of the other ratites from that of *Struthio* because *Struthio* agrees with carinate birds in lacking a vomer-ptyergoid connection. Both Hofer (1945, 1955) and Simonetta (1960) believed that the ratite palate is a uniform structure, but they declined to draw taxonomic conclusions from their data.

Starck (1955) and Lang (1956) assembled evidence from the structure of the brain, palate, and pelvis; the development of the olfactory system; the arrangement of the trigeminal musculature; and mode of reproduction to show that the Apteryges (Apterygidae and Dinornithidae) are widely separated from the other ratites.

The controversy over an independent origin of ratites was reopened by Holmgren (1955) and Glutz von Blotzheim (1958) who believed that carinate birds arose from "generalized" Jurassic coelurosaurs and that ratites evolved from the larger Cretaceous coelurosaurs. DeBeer (1956, 1964) seems to have settled the question with his impres-

sive marshaling of evidence for the derivation of ratites from flying birds. As proof he cited the structure of the wing, the presence of a pygostyle, and the complexity of the ratite cerebellum. He interpreted the palatal structure, the condition of the plumage, and the presence of sutures in the adult skull as neotenic characters associated with the loss of flight.

Eichler (1955) presented a "phylogeny" of the tinamous based upon their Mallophaga. He proposed three subfamilies: Tinaminae (*Tinamus*, *Crypturellus*, *Nothocercus*), Rhynchotinae (*Rhynchotus*, *Taoniscus*, *Nothura*, *Nothoprocta*), and Eudromiinae (*Eudromia*, *Tinamotis*).

Dubinín (1958) summarized his work and the work of others on bird parasites. He emphasized the monophylety of the large ratites and supported a relationship of the Tinamidae to the Galliformes.

The histology of the long bones of birds was studied in detail by Zavattari and Cellini (1956). They found that the ratites (*Struthio*, *Rhea*, and *Casuarius* examined) have a complex Haversian canal system, superficially like that of mammals. Carinate birds show an irregular disposition of the Haversian canals. Tinamous show some differences from both ratites and carinates but were thought by Zavattari and Cellini to be not distant from the ratites. *Apteryx* was not examined.

The egg shells of ratite birds were analyzed with chemical, histological, and plastic-embedding techniques by Tyler and Simkiss (1959). These authors discovered similarities between the egg shells of kiwis and tinamous in chemical composition (amount of magnesium and phosphorus), pore shape, and several other aspects of fine structure. The shells of cassowary and emu eggs were similar, but the egg shells of ostrich and rhea differed from each other and were unlike those of the cassowary and emu.

A paper electrophoretic analysis of egg white proteins (Sibley, 1960) demonstrated close relationship among *Casuarius*, *Dromaius*, and *Struthio*, but a decision on *Rhea* was deferred until additional material was available for study. Sibley found little in the patterns to support a relationship of the tinamous either to the rheas or to the fowls.

Verheyen (1960a, d-f; 1961) discerned a similar structural plan among the large ratites and placed them in a single order next to the Galliformes. He considered the kiwis to be distantly related to penguins and placed them at the base of his linear sequence. In his opinion, the tinamous are closest to the Cracidae.

In his earlier classifications (1930, 1934, 1940) Wetmore followed Pycraft (1900) by placing the seven orders of Pycraft in the superorder Palaeognathae. Following McDowell's (1948) claim that the "palaeognathous" palate was actually composed of four different morphological conditions, Wetmore (1951, 1960) combined the Palaeognathae and Neognathae. Other recent classifications (Mayr and Amadon, 1951; Storer, 1960a) have followed essentially the same course. But none of these authors has adopted McDowell's (1948) suggestion that the tinamous and rheas be placed in the same order.

Cobb and Edinger (1962) studied the brain of the emu and found no reason to consider it primitive compared to that of other birds, but pointed out that comparative gross anatomy of the avian brain offers few clues to relationships.

Behavioral evidence in support of a monophyletic origin for the large ratites, the kiwis and the tinamous was presented by Meise (1963). He considered the magnitude of the differences in behavior among these groups to be no greater than, for example, among the Galliformes.

From a study of the palate W. Bock (1963) also supported the monophylety of the ratites and tinamous. Contrary to McDowell (1948), he reasoned that the

homology of the palaeognathous palate in ratites and tinamous is indicated by the following features:

- 1) The vomer is relatively large, articulating anteriorly with the premaxillae and maxillopalatines and posteriorly (except in *Struthio*) with the pterygoids.
- 2) The pterygoid prevents the palatine from articulating with the basisphenoidal rostrum.
- 3) The palatine articulates with the pterygoid along a suture.
- 4) The basitemporal articulation is large, and near the posterior end of the pterygoid.
- 5) The articulation between the pterygoid and the quadrate is complex, including part of the orbital process of the quadrate.

Wilson et al. (1964) and Kaplan (1965) reported that the palaeognathous birds they examined (*Struthio*, *Rhea*, and a tinamou) all possess lactate dehydrogenases (LDH) of a higher inactivation temperature and greater relative electrophoretic mobility than those of neognathous species. Such characteristics were similar to those found in "higher" reptiles such as the caiman (*Caiman*), a monitor lizard (*Varanus*), and a rattlesnake (*Crotalus*). The properties of tinamou LDH correspond more closely to those of ratite LDH than to those of other groups of birds.

On the basis of an immunoelectrophoretic investigation of egg white proteins, H. Miller and Feeney (1964) noted considerable similarity among the large ratites and suggested the following taxonomic sequence: *Casuarius*, *Dromaius*, *Rhea*, *Struthio*. Whole tinamou egg white showed slight reactivity with an anti-cassowary serum.

Glenny (1965), dissecting mainly immature birds, found the carotid artery pattern of *Apteryx* and the rheas to be B-4-s (unicarotid). In *Struthio* and the *Casuariiformes* it is the bicarotid A-1 arrangement. This indicated to Glenny a close relationship among the ostrich, cassowaries, and emu; he felt that the rheas and kiwis had separate ancestries.

A conformation of the rhamphotheca is shared by the downy young, as well as adults, of the large ratites, the kiwis and the tinamous and is not found in other birds (Parkes and Clark, 1966). This was interpreted as another character showing the monophylety of these groups.

The egg white proteins of *Casuarius casuarius*, *Dromaius novaehollandiae*, *Rhea americana*, *Struthio camelus*, *Apteryx mantelli*, and *Eudromia elegans* were analyzed by Osuga and Feeney (1968). These examinations included electrophoresis of whole egg white, determination of relative quantities of individual components, and comparisons of the biochemical properties of isolated proteins. Although some differences among homologous fractions were noted, "close biochemical and immunochemical relationships were found among the ratites, and they appeared remotely related to the tinamou" (p. 560).

Gysels (1970) examined the electrophoretic patterns and immunodiffusion reactions of the eye lens proteins of some ratites and the tinamous and concluded that they are most like those of *Rhea* but that *Rhea* is even closer to *Casuarius* and that *Casuarius* is closest to the Galliformes.

Sibley and Frelin (in press) compared the egg white proteins of the large ratites, *Apteryx* and several tinamous, using the technique of isoelectric focusing in acrylamide gel. They also compared the tryptic peptides of the ovalbumins of these same groups. The results indicated that the large ratites are more closely related to one another than any one of them is to any other group of living birds, that the kiwis are not closely related to any of the other groups with which they were compared; and that the tinamous are not closely related to any of the large ratites but may be distantly related to the Galliformes.

SUMMARY

Of the two questions posed at the beginning of this chapter, one seems to have been answered from anatomical and embryological evidence. In our opinion, it is clear that the ratites evolved from flying ancestors.

Secondly, the relationship of the large ratites to one another is suggested by a considerable body of evidence that has accumulated from morphological, parasitological, ethological, and biochemical studies. A relationship of the tinamous to the large ratites is suggested by the data on palate and rhamphothecal structures, but the pterylography and Mallophaga suggest an alliance with the gallinaceous birds. Other characters are equivocal. The affinities of *Apteryx*, in spite of all previous studies, are still an enigma.

THE EGG WHITE PROTEIN EVIDENCE

ORDER STRUTHIONIFORMES

FAMILY STRUTHIONIDAE, Ostriches. 1/1, fig. 2.

Species examined: *Struthio camelus*.

ORDER RHEIFORMES

FAMILY RHEIDAE, Rheas. 2/2, fig. 2.

Species examined: *Rhea americana*, *pennata*.

ORDER CASUARIIFORMES

FAMILY CASUARIIDAE, Cassowaries. 2/3, fig. 2.

Species examined: *Casuarius casuarius*, *bicarunculatus*.

FAMILY DROMAIDAE, Emus. 1/2, fig. 2.

Species examined: *Dromaius novaehollandiae* (for the use of *Dromaius* see Serventy, Condon, and Mayr, 1965).

ORDER APTERYGIFORMES

FAMILY APTERYGIDAE, Kiwis. 1/3, figs. 2, 3.

Species examined: *Apteryx australis*.

ORDER TINAMIFORMES

FAMILY TINAMIDAE, Tinamous. 16/33, fig. 3.

Species examined: *Tinamus tao*, *major*; *Nothocercus bonapartei*; *Crypturellus cinereus*, *obsoletus*, *soui*, *cinnamomeus*, *noctivagus*, *tataupa*; *Rhynchotus rufescens*; *Nothoprocta cinerascens*, *pentlandii*, *perdicaria*; *Nothura maculosa*, *darwinii*; *Eudromia elegans*.

RATITES. The starch gel patterns of the egg white proteins evaluated in this paper substantiate and augment the earlier conclusions of Sibley (1960) in several ways. The large ratites are characterized by a fast-moving ovalbumin. It migrates farthest anodally of any ovalbumin from birds thus far studied. In *Struthio*, *Rhea*, *Dromaius*, and *Casuarius* the ovalbumin region contains two bands. The patterns of *Dromaius* and *Casuarius* are quite similar to one another, even to such details as the position of Component 18, which has a fairly high anodal mobility. Both possess five or six conalbumins. These migrate far cathodally in *Casuarius*, and the most cathodal band has the highest concentration. In *Dromaius* the cathodal mobility is somewhat less, and the middle conalbumins are most concentrated.

Struthio differs from *Casuarius* and *Dromaius* only in the shorter distances that its conalbumins migrate cathodally and its Component 18 migrates anodally. Both

species of *Rhea* agree with *Struthio* in the position of nearly all components but differ in having an additional broad band behind the ovalbumin. Whether this band is homologous to the poorly defined bands which appear behind the ovalbumins of *Struthio*, *Casuaris*, and *Dromaius* is not known. The importance of this feature cannot be assessed fully, but it is obvious that the patterns of both species of *Rhea* resemble those of the other large ratites more than they do the patterns of any other group studied. The egg white protein evidence thus supports the proposals of a monophyletic origin for the large ratites.

On the basis of the previous studies and the egg white protein evidence we propose that the large ratites be placed in a single order as follows:

- Order Struthioniformes
 - Suborder Struthiones
 - Family Struthionidae (*Struthio*)
 - Suborder Casuarii
 - Family Casuariidae (*Casuaris*, *Dromaius*)
 - Suborder Rheae
 - Family Rheidae (*Rhea*)

APTERYX. The egg white pattern of the kiwis is unlike those of the large ratites or the penguins, but is somewhat similar to those of tinamous.

The ovalbumin region in *Apteryx* has a mobility similar to that of tinamous, but the pattern is different. In *Apteryx* the most anodal band is the more concentrated whereas in tinamous the middle one of three ovalbumins is in greatest concentration. In *Apteryx* there is a series of fine bands immediately cathodal to the ovalbumins; these are not found in the tinamou pattern. *Apteryx* has its conalbumins clustered in a dense band to the cathodal side of the application point. Tinamous usually have three conalbumins, which migrate cathodally or anodally and may be located to the anodal side of Component 18. A small band migrating to the cathodal side of the conalbumin region in *Apteryx* may be lysozyme.

TINAMOUS. The present study, based on 7 genera and 14 species of tinamous, shows this group to be homogeneous and distinctive. There are several points of dissimilarity between the patterns of tinamous and those of the large ratites. The more slowly migrating ovalbumins of the tinamous, compared to the ratite ovalbumins of high relative mobility, form the most striking difference. The tinamou ovalbumin is distinctly tripartite, a feature not found in the ratite ovalbumins. The mobility of Component 18 in the tinamou pattern is slower than that in the ratite pattern. The mobilities of conalbumins show a resemblance to the homologous bands in *Rhea*, as noted previously by J. Clark, Osuga, and Feeney (1963), but the regions are not identical. Furthermore the variation in the mobilities of conalbumins between members of the same genus, such as *Crypturellus soui* and *C. obsoletus*, *Nothura maculosa* and *N. darwini*, limits the reliability of this character.

The egg white data thus suggests that the tinamous are less closely related to the rheas than the rheas are to the other large ratites.

There are resemblances in the egg white patterns of tinamous to those of gallinaceous birds. In the tinamous the middle component of the tripartite ovalbumin is most concentrated. Some fowls, such as *Phasianus colchicus*, show a similar arrangement and mobilities in the ovalbumin region. In other Galliformes the ovalbumin band farthest toward the anode is the most concentrated. There is at present no evidence that the three ovalbumin components observed in the tinamou pattern are caused by differences in the number of attached phosphate groups, as in the Gal-

lifformes. Other aspects of the galliform pattern, notably the conalbumins and the presence of lysozyme, are different. Further examination of proteins of these groups should be undertaken.

CONCLUSIONS

We conclude that the egg white patterns of the large ratites are more similar to one another than they are to those of any other avian group. From all available evidence it seems likely that these birds were derived from a common ancestor and are more closely related to one another than to any other living group. The pattern of the tinamous differs from those of the large ratites and shows some similarities to those of gallinaceous birds. Considering all evidence, we think that it is more likely that the tinamous are distantly allied to the Galliformes rather than to the large ratites. The egg white pattern of the kiwis (*Apteryx*) is more like those of the tinamous than those of the large ratites, but to suggest a kiwi-tinamou relationship without further supporting evidence is unwise. Although we believe that the large ratites are monophyletic and should be united in a single order, we do not believe that the relationships of the kiwis and tinamous have yet been determined beyond question.

ORDER GAVIIFORMES AND ORDER PODICIPEDIFORMES

Order Gaviiformes
Family Gaviidae, Loons
Order Podicipediformes
Family Podicipedidae, Grebes
Wetmore, 1960

INTRODUCTION

Throughout most of their taxonomic history the loons (or divers) and the grebes have been considered as closely related or as separate but adjacent groups. Thus, most of the literature treats them together; for convenience in discussion we will follow this tradition. Although loons and grebes are superficially similar, profound anatomical differences exist between them. We have summarized these in Table 1.

There are two principal taxonomic questions concerning the loons and grebes. (1) Are they closely related to one another, i.e., monophyletic, or are their similarities solely the result of convergence? (2) To what other group or groups of birds is each next most closely related?

TABLE 1. Principal anatomical differences between loons and grebes

<i>Gavia</i>	<i>Podiceps</i>
Nasal gland large, making a large indentation in skull*	Nasal gland small, making no indentation in skull*
Hind process of lower mandible long	Hind process of lower mandible short or lacking
Dorsal apterium restricted to neck	Dorsal apterium restricted to back
Sternotracheal musculature symmetrical	Sternotracheal musculature asymmetrical
Both carotids present	Only left carotid present
Cervical vertebrae 14 or 15	Cervical vertebrae 17-21
Dorsal vertebrae free	Dorsal vertebrae ankylosed
Sternum twice as long as wide, its posterior border notched on each side	Sternum broad and short, its posterior border notched on either side, and with a triangular notch in middle
11 primaries	12 primaries
Patella lacking	Patella large and pyramidal
Hypotarsus with strong ridges, terminating posteriorly in a triangular open area	Hypotarsus complex, with many canals and grooves
Anterior toes webbed	All toes lobate
Tongue with large patch of spinous processes at base	Tongue with single row of spinous processes

SOURCES: Fürbringer (1888), Gadow and Selenka (1891), Pycraft (1899b), Gardner (1925), and Stolpe (1935).

* The size of the nasal gland is related to the need for salt excretion (Schmidt-Nielsen, 1960) and thus reflects the salt water habitat of *Gavia* versus the fresh water habitat of *Podiceps*.

HISTORICAL REVIEW OF THE CLASSIFICATION

Nitzsch (1840) placed the loons, grebes, auks and penguins in a single group, the Pygopodes, because of similarities in pterylosis. G. Gray (1845) included the loons and grebes as adjacent families between the Anatidae and Alcidae in his order Anseres. Coues (1866b) examined the osteology and myology of *Gavia immer* (= "*Colymbus torquatus*") and concluded that it is most closely allied to the grebes and more distantly related to the Alcidae.

Huxley (1867) united the loons and grebes in a single family, the Colymbidae, which, along with the Alcidae, Procellariidae, and Laridae, made up his Cecomorphae. "The Colymbidae appear to be closely connected on one hand with the Gulls, and on the other, more remotely, but still really, with the Rails" (p. 458).

In Garrod's (1873d, 1874a) system the loons and grebes are adjacent families listed between the Spheniscidae and Procellariidae in his order Anseriformes.

The order Pygopodes of P. Sclater (1880) included the families Colymbidae (for both loons and grebes) and Alcidae. The Pygopodes were placed between the Impennes (penguins) and the Tubinares (Procellariiformes).

Reichenow (1882) united the Spheniscidae, Alcidae, and Colymbidae in his order Urinatores. Stejneger (1885) gave the loons and grebes separate family rank within his order Cecomorphae. This assemblage followed the penguins in his list and included the Heliornithidae, Alcidae, Laridae and Procellariidae.

The suborder Podicipitiformes of Fürbringer (1888) included the Colymbidae (loons) and Podicipidae (grebes) as well as the fossil birds *Hesperornis* and *Enaliornis*. In his phylogenetic tree this group appears closest to the Pelecaniformes and Anseriformes and quite distant from the Procellariiformes, Charadriiformes, or Sphenisciformes.

Seebohm vacillated in his opinion of the relationships of loons and grebes within a single year. He first noted (1888a: 3) that "it is impossible . . . to regard the Grebes as nearly related to the Divers. . . . The arrangement of their palatine bones notwithstanding, there can be little doubt that Grebes are modified Ducks." This apparently firm opinion was soon altered when Seebohm (1888b) stated that the osteological differences between loons and grebes are of minor importance and united the two groups in a single suborder. He dismissed the idea of a close relationship to the Alcidae and thought that the loons and grebes were most closely allied to the penguins. In Seebohm's 1890 classification the loons and grebes, combined as the Pygopodes, are found between the Fulicariae and Gallinae in his order Gallo-Grallae.

The loons and grebes were assigned to separate but adjacent orders by Sharpe (1891), and these orders were placed between his Heliornithiformes and Sphenisciformes.

Gadow (1893) found loons and grebes similar in many respects but was unable to suggest close ties with any other group of birds. He assigned them to his order Colymbiformes near the base of his sequence of carinate birds, followed by the penguins.

Ogilvie-Grant (1898) recognized the loons and grebes as the two families composing his order Pygopodes. The Pygopodes are placed between the Steganopodes and Alcae; the relationships among these groups were not discussed. Beddard (1898a) also treated the loons and grebes as two families, in his order Colymbi. He did not speculate on their nearest relatives. Pycraft (1899b), on the basis of osteology, concluded that loons and grebes are related, but he did not consider them closely allied to the auks or to the gulls.

Goodchild (1891) found that the Colymbidae (presumably referring to both loons and grebes) had an arrangement of their secondary wing coverts similar to that of the Gruidae, Laridae, Phoenicopteridae, Threskiornithidae, and Ciconiidae, among others.

The loons and grebes form a natural group, perhaps derived from a *Hesperornis*-like ancestor, according to Shufeldt (1892; 1904a,b; 1914b). He considered the loons and grebes to be so closely related that he placed them in two subfamilies in the Podicipidae, the only family in the order Pygopodes. Among their closest living relatives, according to Shufeldt, are the Alcidae and Laridae.

Chandler (1916: 301-02) wrote:

The feathers of grebes and loons are very highly specialized and differentiated, and show an almost perfectly intermediate position between penguins on the one hand and Procellariiformes on the other. In the structure of the breast feathers and down, loons come much nearer the Sphenisciformes than do grebes, and they are also more similar to the Procellariiformes. The grebes appear to represent a separate offshoot of the group, and have a condition of the breast feathers which is different from that of any other birds except some of the Alcidae.

Although Gardner (1925) found that modifications of the avian tongue correlated with food habits and generally were of limited taxonomic value, some interesting points emerged from his study. The tongue in the loons differs from that of the grebes, although their food habits are similar. The loons have a large patch of spinous processes at the base of the tongue, but the grebes have only a single posterior row.

Stolpe (1932, 1935) presented evidence from the myology and osteology of the hind limb that loons and grebes are quite different and concluded that the two groups are no more closely related to each other than either is to some other group of aquatic birds. He found important variation in the structure of the cnemial crest. In the loons the cnemial crest is formed by a projection of the tibia, in grebes by a fusion of the patella and tibia, and in *Hesperornis* by the patella alone.

Stolpe pointed out that the movement of the toes in swimming also differs in loons and grebes. Immediately prior to the recovery stroke in swimming the loons flex the toes without rotating them. The grebes rotate the toes through a 90° arc while flexing them so that the longer mesial lobes trail and the shorter lateral lobes fold against the underside of the toe. Stolpe's observations and opinions have had a major influence on subsequent classifications.

Hudson (1937) noted differences as well as similarities in pelvic musculature between loons and grebes. The muscle formula for the common loon (*Gavia immer*) is ABCDXV+; that for the eared grebe (*Podiceps nigricollis*) is BCX. The eared grebe lacks the *M. semimembranosus*, *peronaeus brevis* and *M. flexor perforatus digiti II*, which are present in the loon. However, Storer (1960b: 704) found *M. flexor perforatus digiti II* "present and well developed" in *Podilymbus*. Loons and grebes agree in having the *sartorius* with an isolated insertion on the medial side of the head of the tibia and in having the *pars interna* of the *gastrocnemius* two-headed, arising from a long line down the proximal half of the tibia.

E. Stresemann (1927-34) attributed the similarities between loons and grebes to convergence and recognized no obvious ties between either group and other avian orders. Maintaining the loons and grebes in separate but adjacent orders are Peters (1931) and Wetmore (1930, 1934, 1940, 1951, 1960).

Mayr and Amadon (1951: 5) were aware of Stolpe's (1935) conclusions but kept the loons and grebes near one another in their classification because "the grebes

have been thought to be remote allies of the petrels, and since McDowell (oral communication) thinks that the loons may be a specialized offshoot of petrel stock, it is possible that the grebes and loons have some distant or indirect relationships."

The Oligocene fossil *Colymboides minutus* was considered to be intermediate between loons and grebes by its describer, Milne-Edwards (1867-71) and by Howard (1950: 5), who believed that "there is no doubt that the diving birds, the grebes and loons, stem from a common ancestor. . . ." Storer (1956), however, in reevaluating *Colymboides*, judged it to be an ancestral loon. He also noted (p. 425): "The coracoid of loons is most similar to that of shorebirds and gulls, and birds of these groups also have two proximal foramina on the tarsometatarsus and three anterior hypotarsal canals. Thus, the loons may have their closest relationship with the great charadriiform complex."

Storer (1960b) emphasized the differences in the cnemial crest, pelvic musculature, and foot structure between loons and grebes. "The Hesperornithes, the loons and the grebes are outstanding examples of convergent evolution. In fact, I doubt that they even had a common swimming ancestor" (p. 701).

Brodkorb (1963b) proposed the new family Lonchodytidae in the Gaviiformes to accommodate *Lonchodytes estesi* and *L. pterygius* of Upper Cretaceous age from Wyoming. Although this discovery greatly increased the known antiquity of the loons, Brodkorb did not comment on comparisons other than the obvious one to *Gavia*.

Storer (1963a,b; 1967a,b; 1969) studied the behavior of grebes to clarify the relationships within the family. Other aspects investigated include the osteology and myology of the head and neck of the genus *Podilymbus* (Zusi and Storer, 1969) and the patterns of the downy young (Storer, 1967a). May (1945) and J. Niethammer (1964) also have compared the plumage patterns of the downy young of some species of grebes. The conclusions based on the behavioral evidence and those from the plumage pattern of the downy young are concordant. Storer (1967a) divided the grebes into three groups. The first of these includes *Podiceps* (*major*, *griseogena*, *cristatus*, *auritus*, *nigricollis*, *occipitalis*, and *taczanowkii*) and *Aechmophorus occidentalis*. A second group is composed of *Rollandia* [= *Podiceps*] *rolland* and *R. microp-terum*. The third group is made up of four species of *Tachybaptus* (*ruficollis*, *novae-hollandiae*, *pelzelni*, and *rufolarvatus*). Storer felt that the remaining three species—*dominicus*, *rufopectus*, and *poliocephalus*—probably should belong in *Tachybaptus* rather than in *Podiceps*, on the basis of downy young plumage, but their behavior is insufficiently known.

Verheyen (1959c) was impressed by osteological similarities between the grebes and the sun-grebes or finfoots (Heliornithidae) and placed the grebes as a suborder in his order Ralliformes between the suborders Grues and Ralli. In his opinion, the loons belong in the Alciformes with the Alcidae and Pelecanoididae. Verheyen (1961) did not change his thoughts on the relationships of the Gaviidae, but he gave the grebes ordinal rank, feeling that they were allied on one hand to the Ralliformes (Rallidae, Heliornithidae) and on the other to the Jacaniformes (Jacanidae, Eurypygidae, Rhynochetidae, Mesitornithidae).

Comparing the paper electrophoretic patterns of the loons and grebes, Sibley commented: "There is little to indicate a grebe-petrel relationship and not much to support a grebe-loon alliance. Thus, other than showing that the grebes are surely monophyletic (which was not in doubt), the egg-white profiles give us little new information about their affinities" (1960: 231). On the other hand, the egg white patterns of the loons resembled those of the gulls most closely, and for this reason Sibley placed "the Gaviiformes near the Charadriiformes rather than in their usual place near the grebes" (p. 234).

The presence of a cover (a layer of material lying above the cuticle) and lack of

pigmentation in the egg shells of grebes differentiates them from those of the loons (Tyler, 1969). He also found differences between the shells of eggs from the two groups in the amounts and distribution of true shell nitrogen and in histological staining. Tyler did not find any similarities between the egg shells of grebes and those of Procellariiformes, and he was unable to suggest any possible relatives for either the loons or the grebes.

SUMMARY

The loons and grebes are two small, distinctive groups of birds. They share numerous characters of osteology, myology, and pterylosis, which has led a majority of workers to conclude that the two groups are closely related. Since the work of Stolpe it has become customary to regard these similarities as due to convergence. Other groups suggested as relatives of either or both the loons and grebes are, in order of decreasing frequency, the Alcidae, Spheniscidae, Heliornithidae, Pelecaniformes, Procellariiformes, Laridae, and Anseriformes.

THE EGG WHITE PROTEIN EVIDENCE

ORDER GAVIIFORMES

FAMILY GAVIIDAE, Loons or Divers. 3/4, fig. 3.

Species examined: *Gavia immer*, *arctica*, *stellata*.

ORDER PODICIPEDIFORMES

FAMILY PODICIPEDIDAE, Grebes. 10/19, fig. 4.

Species examined: *Podiceps ruficollis*, *dominicus*, *auritus*, *nigricollis*, *cristatus*, *griseogena*, *poliocephalus*, *rolland*; *Aechmophorus occidentalis*; *Podilymbus podiceps*. (The nomenclature is altered from that of Peters, 1931, with *Podiceps* replacing *Colymbus* [see Salomonsen, 1951] and *Poliocephalus* being merged with *Podiceps* [Wetmore, 1939: 180]).

The starch gel patterns of the egg white from the three species of *Gavia* are similar. In all aspects these patterns are identical to those of shore birds, particularly the Laridae and Alcidae. The loon patterns are also similar to those of some Procellariiformes and hence to those of the penguins, but they differ slightly in the mobility of the ovomucoid.

The egg white patterns of the grebes differ in minor but consistent points from those of the loons. The conalbumins of grebes migrate anodal to Component 18. This may be seen clearly in the patterns of *Podiceps ruficollis* and *cristatus* (fig. 4). In loons the conalbumins are seen between the application point and Component 18. The ovomucoid of grebes has a greater relative mobility anodally than that of loons. In the patterns of some grebes, such as *Podilymbus podiceps*, it migrates so close to the "tailing" of the ovalbumin that the two proteins seem almost to merge. The ovalbumin region in the patterns of grebes contains two components, the anodal one being smaller and slightly less concentrated. This contrasts with the loon pattern, where only a single ovalbumin is present. The ovalbumins of both loons and grebes, however, have similar mobilities. In some patterns of grebes a prealbumin is present, which is not seen in the patterns of the loons.

With this combination of features it is possible to separate the patterns of the

grebes from those of loons, but the fact remains that the patterns are similar. The patterns of the grebes contain similarities to those of some Procellariiformes, Sphenisciformes, and Charadriiformes. The grebes agree with some penguins and shearwaters in the position of the conalbumins and the possession of a prealbumin but differ in the position and concentration of ovomucoid. In most Procellariiformes the ovomucoid migrates farther behind the ovalbumin and is less concentrated (see *Procellaria* and *Puffinus* among others, fig. 5). The shorebirds, as well as the loons, differ in having a slightly faster ovalbumin, the anodal edge of which has a distinctive "squared off" appearance (e.g., *Larus*, figs. 23, 24). The ovomucoid is present in rather low concentration and in some species it is composed of more than one band. The conalbumins of shorebirds, loons, and rails characteristically migrate behind Component 18, and almost invariably there is no prealbumin. The egg white patterns of grebes, therefore, although resembling those of several groups of aquatic birds, do not strongly suggest an alliance with any of these groups.

CONCLUSIONS

The total available evidence indicates to us that the loons and grebes are members of the large complex of aquatic non-passerine birds, and that each of them is probably more closely related to some other group than to each other. The closest living relatives of the loons seem to be the shorebirds (Charadriiformes); the closest relatives of the grebes remain uncertain.

ORDER PROCELLARIIFORMES

Family Diomedidae, Albatrosses
Family Procellariidae, Shearwaters, Fulmars
Family Hydrobatidae, Storm-Petrels
Family Pelecanoididae, Diving-Petrels

Wetmore, 1960

INTRODUCTION

All members of the Procellariiformes have tube-shaped nostrils. This feature alone distinguishes the procellariiforms from other groups. That they represent a natural assemblage has seldom been doubted. Thus, the principal line of taxonomic inquiry has been concerned with the allocation of genera and the relationships among the various groups within the order. The second problem deals with the relationships of the Procellariiformes to other avian orders, about which little has been written. The evidence for a sphenisciform-procellariiform alliance has been discussed above, under the penguins, and will be mentioned only briefly here.

HISTORICAL REVIEW OF THE CLASSIFICATION

The Procellariiformes were placed between the Laridae and the Anatidae by Nitzsch (1840). A relationship to the gulls was considered likely by Gray (1845), who thought that the Procellariiformes might also be allied to the penguins and alcid.

Coues (1864, 1866a) provided the first important monograph of the order. His work was criticized for lacking an adequate series of specimens and first-hand field observations, but it was valuable in many respects. The classification proposed by Coues is as follows:

Family Procellariidae
Subfamily Procellariinae

- "Group" Procellariidae (= storm-petrels)
- "Group" Puffinae
- "Group" Fulmaridae
- "Group" Aestrelatae
- "Group" Prionidae
- Subfamily Diomedidae
- Subfamily Halodromidae (= diving-petrels)

Huxley (1867) included the procellariiform birds, along with the Laridae, Colymbidae (loons and grebes), and Alcidae, in his Cecomorphae. Only a single family, the Procellariidae, was recognized, which differed from the others in this assemblage by a greater expansion of the maxillopalatines, a stronger ventral bend in the anterior portion of the vomer, and an increase in size of the ascending process of the palatine so that it is ankylosed with the vomer. Huxley felt that *Procellaria gigas* (= *Macronectes giganteus*) was intermediate between the albatrosses and the gulls, and he saw similarities among the Procellariidae, Phalacrocoracidae, and Pelecanidae.

The procellariiform groups were included in Garrod's order Anseriformes, which also contained the loons, grebes, penguins, and ducks (1873d, 1874a). P. Sclater (1880) placed his order Tubinares between the Gaviae (gulls) and Pygopodes (loons, grebes, alcids).

In the list of Stejneger (1885) the procellariiform birds followed the gulls in the order Cecomorphae. This group also included the Alcidae, Heliornithidae, Gaviidae, and Podicipedidae.

Forbes (1882e) reported on the anatomy of the Procellariiformes obtained during the *H.M.S. Challenger* Expedition (1873-76) and proposed a classification in which two families—the Oceanitidae (storm-petrels) and the Procellariidae—were recognized. The latter group contained the albatrosses as a subfamily, but *Pelecanoides* was given only generic distinction within the Procellariinae.

Garrod (1881) included *Pelecanoides* in his Oestrelatinae because it possesses the semitendinosus muscle. This subfamily of the Procellariidae also encompassed the genera of the Diomedidae and Procellariidae of Wetmore's (1960) list. *Pelecanoides* differs from most petrels, except *Bulweria*, in lacking an accessory femoral-caudal muscle. Garrod (1881) also changed his earlier opinion and suggested that the Ciconiiformes are the closest allies of the Procellariiformes.

Fürbringer (1888) listed the Procellariiformes after the Ciconiiformes (= Phoenicopterii, Pelargo-herodii, Accipitres, Steganopodes) and the Impennes (penguins) and before the Charadriiformes.

The Procellariiformes belong between the Galliformes and Impennes, fairly close to the gulls but far from the Pelecaniformes and Ciconiiformes (Seebohm, 1890). In Sharpe's arrangement (1891) the Procellariiformes were placed between the Sphenisci and the Alcae. He thought that a slightly more distant relationship to the gulls was possible, but that the Ciconiiformes and Pelecaniformes belonged far from the petrels.

Gadow (1892, 1893) put the Procellariiformes between his Sphenisciformes (penguins) and Ardeiformes (pelicans, herons and storks). In his system the Charadriiformes, including the gulls, are distant from the Procellariiformes.

In Salvin's (1896) system the Tubinares followed the Gaviae (gulls). He recognized the families Procellariidae (storm-petrels), Puffinidae (shearwaters, etc.), Pelecanoididae, and Diomedidae.

In the classification by Pycraft (1899a) only the families Diomedidae and Procellariidae were recognized. The latter group was made up of the Procellariinae and Pelecanoidinae. Godman (1907-10) monographed the order and followed the classification proposed by Salvin (1896).

In the structure of the feathers Chandler (1916) found "unmistakable resemblances to the Colymbiformes, especially the loons." He thought that *Diomedea* was the most specialized of the Procellariiformes and that a primitive member of the order may have given rise to the Ciconiiformes through the Pelecaniformes.

Coues (1897) modified his 1864 and 1866a classification to produce the following arrangement:

- Order Tubinares
 - Family Diomedidae
 - Family Procellariidae
 - Subfamily Fulmarinae
 - Subfamily Puffininae
 - Subfamily Procellariinae
 - Subfamily Oceanitinae
 - Family Pelecanoididae

In his review of the Procellariiformes, Loomis (1918) was guided by the works of Coues, Salvin, and Godman, and made only minor changes for his classification. He did not discuss the relationships of the Procellariiformes to other groups. In 1923 he modified his classification and presented one that is nearly identical to that in use today (e.g., Wetmore, 1960).

Lowe (1925a) made comparisons only within the order. He used characters of the quadrate and adjacent bones to divide the order into two families. The Oceanitidae, which he thought to be more generalized or "primitive", included the genera *Oceanites*, *Pelagodroma*, *Fregetta*, *Garrodia*, *Thalassidroma*, *Cymochorea*, *Oceanodroma*, and *Halocyptena*. The remaining genera, including *Pelecanoides*, were placed in the Procellariidae, and two subfamilies, for the albatrosses and shearwaters, were recognized.

E. Stresemann (1927-34) admitted a procellariiform-sphenisciform alliance, but was uncertain about the relationships of the Procellariiformes to any other water bird group.

In his classifications of the Procellariiformes, Mathews (1934, 1935, 1936a,b, 1937) carried splitting to the extreme by recognizing 52 genera for about 75 species. He admitted the usual four families within the order. In 1948 Mathews swung to the other extreme and recognized only 12 genera.

C. Fleming (1941) considered the probable evolution of the six species of *Pachyptila*, and Voous (1949) examined the relationships and evolutionary history of the fulmars.

Except for a penguin-petrel relationship, Mayr and Amadon (1951) found no close relatives of the Procellariiformes. They reduced the storm-petrels and shearwaters to subfamily rank within the Procellariidae.

Kuroda (1954) developed a classification of the Procellariiformes based on a detailed study of skeletal and other morphological characters and on an analysis of adaptations to aerial and aquatic propulsion. Of his conclusions, the most relevant to the present discussion may be summarized as follows:

- 1) The Diomedidae, on the basis of some skull characters and manner of flight, seem to be related to the more aerial members of the Puffininae (e.g., *Calonectris*).
- 2) On the same basis the Hydrobatidae appear closely allied to the Fulmarinae of the Procellariidae.
- 3) The Pelecanoididae form a distinctive and primitive group that shares some skeletal and anatomical characters with both the Hydrobatidae and Procellariidae.
- 4) Principally on skull characters the gadfly-petrels (*Pterodroma*) are more

similar to the fulmars and prions (Fulmarinae) than they are to other Procellariidae.

Kuroda believed that the Procellariiformes descended from aquatic ancestors, and did not question the evidence for a relationship to the penguins. Two osteological characters, mainly present in a reduced state in extant procellariiform birds, suggested to him a former diving habit. One of these is the presence of well-developed hypophyses on the dorsal vertebrae, providing additional attachment for the *M. longus colli anticus*, thus enabling more powerful movement of the neck. The other, the *processus rotularis* of the tibia, provides extra area for the insertion of the thigh muscles and is important in swimming. This "is a remarkable characteristic of the Pygopodes [loons and grebes], shared only by the Tubinares, providing probably their remote relationship in the early Cretaceous . . ." (p. 38).

Verheyen (1958c) recognized the Diomedidae, Procellariidae and Hydrobatidae in his order Procellariiformes. He believed the similarities between the diving-petrels and the auks are due to close relationship rather than convergence (1958d, 1961b). His comparisons were based on skeletal measurements analyzed in a statistically crude fashion and expressed as percentages of characters held in common. This showed that *Pelecanoides urinatrix* and *Plautus alle* (Alcidae) were similar in 65% of 105 skeletal characters. As additional evidence Verheyen noted that both groups have a simultaneous molt of the primaries. This molt pattern is, of course, found in many other water birds (ducks, rails, loons, grebes, flamingos, anhingas) and is an adaptive response to the aquatic habitat, not a reflection of phyletic relationship. Verheyen (1961b: 17) disagreed with Cain (1959: 314) and Wetmore (1960: 6) in their allocation of *Pelecanoides* to the Procellariiformes: "How can we agree when the necessary information to verify the suggested relationships between the Diving Petrels and the Procellariiformes is completely lacking in their papers?"

In his final classification (1961) Verheyen stated that although he believed the auks and their allies to be the nearest relatives of the Procellariiformes, "they are more distantly allied with the Sphenisciformes . . ." (p. 17). The Sphenisciformes, Procellariiformes and Alciformes were arranged together in the superorder Hygromithes.

Sibley (1960) found that six species of the Procellariidae showed similar egg white protein patterns in paper electrophoresis. On resemblances to other groups he wrote (p. 233): "The egg-white profiles show general resemblances to some Pelecaniformes, some Ciconiiformes, some Charadriiformes and some Anseriformes. Nevertheless the profiles of the Procellariidae are clearly different from all of these and a choice is not possible."

The lenticular proteins of the fulmar (*Fulmarus glacialis*) were examined by Gysels (1964a). He was unable to corroborate a relationship to the penguins, and decided that the lens electrophoretic pattern is of the "charadriiform type." The presence of glycogen in the lens he interpreted as an "advanced" character, therefore *Fulmarus* could not be associated with the "lower" non-passerine groups. He concluded: (1) *Fulmarus* is not a procellariiform and belongs instead in the Charadriiformes; (2) the entire order Procellariiformes belongs next to the Charadriiformes; (3) the Procellariiformes are polyphyletic, with some members closest to the shorebirds. Sibley and Brush (1967) declined to accept Gysels' conclusions because their own studies of lens proteins revealed a tendency for rapid denaturation and a high degree of similarity in electrophoretic properties among all birds.

In a monograph on the Mallophaga of the Procellariiformes, Timmermann (1965) strongly rebutted the criticisms directed at the use of parasites as indicators of the taxonomic relationships among host species, and discussed the problems of interpretation. His conclusions on procellariiform relationships were as follows:

- 1) *Pelecanoides* is properly placed within the Procellariiformes (p. 197-98).

2) The Procellariiformes are most closely related to the Charadriiformes, and both *Phaethon* and *Fregata* are also related to the procellariiform birds (p. 203-07).

3) There is no support for a relationship between the Procellariiformes and the Ciconiiformes or the Falconiformes.

4) A sphenisciform-procellariiform relationship is not supported by the Mallophaga or the tapeworms. Although penguins and petrels have a similar tapeworm fauna (Baer, 1954a,b; 1955; 1957), whales are also hosts to the same tapeworm genera (p. 209).

Timmermann (1965: 203-04) cited Verheyen (1960b) in support of his decision that the Procellariiformes are related to *Phaethon* and to the Charadriiformes, particularly the gulls (*Larus*).

Using paper electrophoresis L. E. Brown and Fisher (1966) examined the serum proteins and hemoglobins of several procellariiform birds. They found that the genera *Diomedea*, *Puffinus*, and *Pterodroma* were distinguishable on the basis of their serum proteins, although members of the same genus were identical. The hemoglobins of the albatrosses differed in the concentrations of both components from those of the Procellariidae examined.

Hamlet and Fisher (1967) reported minor variations among the air sacs of *Diomedea immutabilis*, *Puffinus pacificus*, and *P. nativitatis*; the absence of pneumatization of the ribs and coracoid in the procellariids is due to the smaller size of the birds. The lack of the diverticulum esophago-tracheale in the species of *Puffinus* seemed to be the only major difference between the two groups.

Tyler compared the structure of the egg shells of 16 procellariiform species representing all four families. "There are no differences of any consequence in the total true shell nitrogen nor in its fractions between any genera in the order. Similarly the histological staining results for different layers of the shell and all other criteria used failed to reveal any differences" (1969: 410). Tyler did not find any resemblances to the egg shells of penguins, noting particularly that the Procellariiformes lack the shell cover which is typical of the shells of the Sphenisciformes.

SUMMARY

Many authors have suggested that the Procellariiformes are most closely allied to the penguins. Others have thought that the procellariiforms are related to the Alcidae or the Laridae, but they did not always consider the Alcidae and Laridae to be related to each other. Next most frequently suggested as close allies of this order are the Gaviidae and Podicipedidae. Also mentioned as more distant relatives have been the Anatidae, Pelecaniformes and Ciconiiformes.

The genus *Pelecanoides* has been declared to be an alcid and its similarities to the Procellariiformes due to convergence, but the consensus is that *Pelecanoides* and the Alcidae are only convergently similar and that *Pelecanoides* is a procellariiform.

THE EGG WHITE PROTEIN EVIDENCE

ORDER PROCELLARIIFORMES

FAMILY DIOMEDEIDAE, Albatrosses. 7/13, fig. 4.

Species examined: *Diomedea exulans*, *nigripes*, *immutabilis*, *melanophris*, *bulleri*, *chrysostoma*; *Phoebetria palpebrata*.

FAMILY PROCELLARIIDAE, Shearwaters, Petrels. 17/53, fig. 5.

Species examined: *Macronectes giganteus*; *Daption capensis*; *Fulmarus glacialis*; *Pachyptila desolata*; *Procellaria aequinoctialis*; *Puffinus diomedea*, *carneipes*, *pacificus*, *griseus*, *nativitatis*, *puffinus*, *lherminieri*; *Pterodroma alba*, *mollis*, *phaeopygia*, *leucoptera*; *Bulweria bulwerii*.

FAMILY HYDROBATIDAE, Storm-Petrels. 6/20, fig. 5.

Species examined: *Oceanites oceanicus*; *Pelagodroma marina*; *Fregatta tropica*; *Hydrobates pelagicus*; *Oceanodroma leucorhoa*, *castro*.

FAMILY PELECANOIDIDAE, Diving-Petrels. 2/4, figs. 5, 6.

Species examined: *Pelecanoides garnoti*, *georgica*.

The procellariiform birds share a starch gel pattern that is remarkably uniform in all of the species examined. Some minor variation in the mobilities of the ovomucoids may be seen and the conalbumins vary in position, e.g., in the patterns of the albatrosses (Diomedidae) they migrate between the application point and Component 18. In most other procellariiform species the conalbumins migrate anodal to Component 18. In light of previous studies perhaps the most interesting genus is *Pelecanoides*. The patterns of *Pelecanoides garnoti* and *P. georgica* are like those of the Procellariidae. In several gels the pattern of *Pelecanoides* is identical to that of the prion *Pachyptila desolata*. The pattern of *Pelecanoides* is similar to those of the Alcidae but there are consistent differences in the mobilities of the conalbumins and ovomucoids, both components migrating more slowly in the alcids.

As noted above, the patterns of the Procellariiformes are most similar to those of the penguins and somewhat less similar to those of the loons. The general procellariiform pattern also is like that of the Charadriiformes, and among the Pelecaniformes resemblances are seen to the patterns of *Fregata*, *Phaethon*, and *Pelecanus*. The occurrence of a relatively simple egg white pattern among a number of aquatic non-passerine birds poses difficulties in interpretation. One possibility is that the similarities among these patterns reflect a common ancestry of some or all of these groups. The other possibility is that there are rather large differences in the amino acid sequences in the homologous proteins of the various groups that do not affect the net charge on the molecule. Hence, the electrophoretic patterns may be coincidentally similar and are not necessarily reflecting the actual genetic differences between the taxa. Either alternative is intriguing, and it is apparent that more detailed studies are necessary to determine the closest relatives of each group involved.

CONCLUSIONS

The Procellariiformes are a monophyletic group of birds. This is demonstrated by the egg white protein evidence and is supported by a large array of previous evidence from a variety of sources. Because of the uniformity of the starch gel patterns it is not possible to speculate upon relationships within the order. The egg white pattern of *Pelecanoides* is indistinguishable from those of some petrels. From this evidence and from that of previous studies we conclude that *Pelecanoides* is more closely allied to the Procellariiformes than to any other group. The Procellariiformes appear to be allied to the Sphenisciformes, and they may be related to some or all of the following groups: Charadriiformes, *Gavia*, *Fregata*, *Phaethon*, *Pelecanus*.

ORDER PELECANIFORMES

Suborder Phaethontes

Family Phaethontidae, Tropicbirds

Suborder Pelecani

Superfamily Pelecanoidea

Family Pelecanidae, Pelicans

Superfamily Suloidea

Family Sulidae, Boobies, Gannets

Family Phalacrocoracidae, Cormorants

Family Anhingidae, Snakebirds

Suborder Fregatae

Family Fregatidae, Frigatebirds

Wetmore, 1960

INTRODUCTION

The only obvious anatomical character shared by all members of the Pelecaniformes and not found in other groups is the totipalmate feet. All pelecaniforms except *Phaethon* have a gular pouch. They vary considerably in pelvic musculature, carotid artery arrangement and several other characters. In all species the palate is desmognathous, a condition shared with the Ciconiiformes, Anseriformes, Falconiformes and Cariamae (Gruiformes). The furcula is ankylosed to the sternum in *Pelecanus* and connected to it by ligaments in *Anhinga*, *Phalacrocorax* and *Sula*. In *Phaethon* the clavicles attach to the keel. Beddard (1898a) and E. Stresemann (1927-34) provide a more extensive list of anatomical characters but those above illustrate the exceptional diversity among the totipalmate birds. Such diversity raises the question of possible polyphyly, although Beddard believed that the "naturalness" of the order "can hardly be doubted" (1898a: 402). The totipalmate foot defines the group but it would not be surprising if it were shown that this foot structure had evolved more than once, as has the palmate condition.

The questions concerning the Pelecaniformes are therefore clear. First, is the order as presently constituted in the classifications of Mayr and Amadon (1951) and

Wetmore (1960) composed of groups more closely related to one another than any one of them is to some group outside of the order? Second, what are the degrees of relationship among the genera of peleciform birds? The principal doubts on the first question concern *Phaethon* and *Fregata*. In the following review of the literature the evidence concerning these questions will be presented.

HISTORICAL REVIEW OF THE CLASSIFICATION

Nitzsch (1840: 148) wrote that the group of peleciform birds "has a very persistent type of pterylosis, and presents no generic differences, except, perhaps, a variation in the density of the plumage, which appears to be dependent on the climates in which the birds live. . . ." He found that *Pelecanus* somewhat resembled the Anseriformes in its pterylosis and that *Anhinga*, with small apteria, approached the condition in the penguins.

Huxley (1867) did not question that the Peleciformes (his "Dysporomorphae") formed a natural assemblage. The pelicans, forming one "group" within the Dysporomorphae, have considerable development of the inferior edge of the interorbital septum and an enlargement of an ascending process of the palatines. The "remaining genera," composing the second group, were said to lack these features but they were not figured or discussed.

Differences in the pelvic musculature among the Peleciformes were reported by Garrod (1873d, 1874a). In his opinion, *Sula*, *Phalacrocorax*, and *Anhinga* form one family; each of the other groups requires separate family status. He saw similarities between *Phaethon* and the Ciconiiformes on one hand and between *Fregata* and the Falconiformes on the other. He also published two papers (1876d, 1878b) on the anatomy of *Anhinga* in which he described the modified cervical vertebrae associated with their fish-spearing behavior.

Mivart's study (1878) of the postcranial osteology of the Peleciformes concluded that *Pelecanus*, *Sula*, *Phalacrocorax*, and *Anhinga* form a natural group. He was unable to find good characters uniting *Phaethon* and *Fregata* with those four, although the two groups were similar in the number and shape of the vertebrae of each body region and in aspects of the pelvis. Mivart did not speculate upon the closest relatives of *Fregata* and *Phaethon*.

P. Sclater (1880) recognized five families within his Steganopodes and placed the order between his Accipitres and Herodiones (= Ciconiiformes).

Although Stejneger was influenced by Mivart's (1878) paper, he did not entirely accept its conclusions. He commented (1885: 180):

Mivart has shown that the four supergenera . . . [*Pelecanus*, *Sula*, *Phalacrocorax*, *Anhinga*] are more intimately related *inter se* than to the two other ones [*Phaethon*, *Fregata*]. These two, on the other hand, chiefly agree to differ from the former four in negative points, and hence their exclusion from these does not indicate any particular mutual intimacy. On the contrary, the tropic-birds and the frigate-birds are as different between themselves as each of them is from the rest.

Stejneger declined to split the order and instead erected the superfamilies Pelecanoideae, Fregatoideae, and Phaethontoideae to emphasize the differences among the groups. He contended that this order is "unquestionably nearly related to the Herodii" (p. 179).

In his study of intestinal convolutions, Gadow (1889) found evidence to link the Pelecaniformes to the Ciconiiformes and also to the Procellariiformes. In his final paper on this subject (1893), Gadow concluded that the Pelecaniformes were allied to the Ciconiiformes through the storks and to the diurnal birds of prey through the Cathartidae.

Shufeldt published several papers on the osteology of the Pelecaniformes (1883a, 1888b, 1894a, 1902a). He believed that these birds formed a natural assemblage and he recognized three suborders: Pelecanoidea, Phaethontoidea, and Fregatoidea. Skeletal similarities between *Phaethon* and *Puffinus* were noted, as well as possible affinities between *Phaethon* and the gulls. In his opinion, *Fregata* is more similar to *Phaethon* than to other pelecaniforms in features of the pelvis, and its skull is in many ways like that of *Diomedea*.

Fürbringer (1888) placed the pelecaniform birds in his suborder Ciconiiformes and divided them into four families: Phaethontidae, Phalacrocoracidae, Pelecanidae, and Fregatidae. The suborder also included the flamingos, ciconiiforms, and falconiforms.

Seebohm's Steganopodes was divided into five families, with *Anhinga* included in the Phalacrocoracidae (1889, 1890, 1895). He thought that the genera *Phalacrocorax*, *Anhinga*, and *Sula* are the most closely related and that the nearest allies of the pelecaniforms are the Ciconiiformes. Beddard (1898a) agreed with Seebohm that the closest relatives of the Pelecaniformes are the Ciconiiformes but he also put the Procellariiformes in that category.

Sharpe's order Pelecaniformes contained five suborders. In his diagram of supposed relationships (1891) the Pelecaniformes are allied to the Falconiformes through *Fregata*. He also suggested that the Pelecaniformes are related to the waterfowl (Anseriformes).

In his analysis of the intestinal convolutions, Mitchell (1901a) considered that the Pelecaniformes formed a central group, the "steganopod metacentre," from which could be derived the patterns of intestinal convolutions of the Procellariiformes, Ardeidae, Ciconiidae, and Falconiformes. He was careful to point out that the phylogeny of the intestinal tract did not necessarily reflect that of the groups themselves.

Pycraft (1898b) defended the uniformity of the "Steganopodes" on the basis of osteological evidence and (1907a: 24) suggested that the Pelecaniformes were the "common ancestral stock from which have descended the Sphenisci, Colymbi, and Tubinares, on the one hand, and the Ciconiae, Accipitres, and Anseres on the other." He cited as some of his evidence "the nature of the relations between the squamosal and parietal before their fusion, and the nature of the palate at the same period."

Regarding feather structure Chandler (1916: 315) wrote: "The Steganopodes are a group of birds in which primitive characters are curiously combined with specialized characters, the result being a rather heterogeneous aggregation of more or less related forms which are specialized along different lines. They seem to fall into three fairly well-defined groups as follows: (1) *Phalacrocorax*, *Fregata*, *Sula*, and *Pelecanus*; (2) *Plotus* [= *Anhinga*]; and (3) *Phaëthon*." Of these Chandler thought that the first group was the least specialized and had ties with both the Procellariiformes and Ciconiiformes. In the feather structure of *Anhinga* he saw "striking similarity" to that of the Cathartidae and concluded that the cathartid vultures had been derived from a pelecaniform ancestor. *Phaëthon* is not allied to the other Pelecaniiformes, in Chandler's opinion, and should be considered an "aberrant larid form."

The difference between *Phaëthon* and the other Pelecaniformes was emphasized by Mathews and Iredale (1921), and they placed this genus in the suborder Phaethontiformes of their order Lari. Lowe (1926) disagreed with this conclusion and pre-

sented evidence, mainly from the structure of the quadrate, that *Phaethon* is allied to the other Pelecaniformes.

E. Stresemann felt that although the nearest relatives of the Pelecaniformes were uncertain, a distant affinity to the Ciconiiformes or Falconiformes was possible (1927–34: 804). He placed the cormorants and anhingas in separate subfamilies in the Phalacrocoracidae (p. 799).

Lanham (1947), like others before him, weighed the evidence for and against splitting the Pelecaniformes. In spite of the diversity among pelecaniform birds, he concluded that the order is a natural one and assigned *Phaethon* and *Fregata* to the separate suborders distinct from the Pelecani. Similarities among *Sula*, *Phalacrocorax*, and *Anhinga* led him to recognize a superfamily Sulides separate from the Pelecanides. He thought the nearest relatives of the Pelecaniformes are the Procellariiformes.

Howard (1950) developed her thoughts on the relationships of the Pelecaniformes mainly from the fossil evidence. She felt that the Upper Cretaceous *Eoalpteryx* and the Eocene *Eostega* were perhaps ancestral to the Phalacrocoracidae and the Sulidae. The Eocene *Prophaethon* provided a link between the cormorant-sulid stem and the tropicbirds. The Miocene *Cyphornis*, the type of the extinct family Cyphornithidae, showed similarities to the cormorants, sulids, anhingas, and pelicans. Brodkorb (1963a) concurred in recognizing *Eoalpteryx* and *Eostega* as sulids.

Phaethon is less closely related to *Pelecanus* and its allies than is *Fregata* (Mayr and Amadon, 1951). Like Stresemann, these writers gave *Anhinga* only subfamily status within the Phalacrocoracidae. (They incorrectly stated [p. 6] that Stresemann [1927–34: 799] did not accord subfamily status to the cormorants and anhingas.)

The Pelecaniformes of Verheyen (1960b,c; 1961) included the suborders Pelecani, Sulae, and Anhingae (= Anhingidae and Phalacrocoracidae). He classified the Fregatae and Phaethontes as suborders in his order Lariformes, which included as its third suborder the Lari (gulls, terns, skimmers, jaegers). Accordingly, he began the sequence of his superorder Limnornithes with the orders Pelecaniformes, Lariformes and Charadriiformes. He also supported a relationship between *Phaethon* and the Procellariiformes.

The young of *Phaethon* are covered with down and the adults possess a series of air cells under the skin in the front of the body (Wetmore, 1960). In *Fregata* the young are nearly naked at hatching, and the air cells are lacking in adults. On the basis of these differences and those of internal anatomy Wetmore gave each group subordinal rank and placed them on either side of the suborder Pelecani, which contained the remaining genera. The anhingas were given family rank because they "are marked by a peculiar conformation of the cervical vertebrae through which the beak becomes a triggered spear in feeding. The bridge of Dönitz on the ninth vertebra is an important part of this arrangement. The stomach also is unusual in possessing a curious pyloric lobe, lined with a mat of hair-like processes. And there is only one carotid artery while in cormorants there are two" (p. 7–8).

There are "marked dissimilarities" among the egg white patterns of the Pelecaniformes (Sibley, 1960). The patterns of *Phaethon* and *Fregata* were similar but differed from those of others in the order. Sibley also noted (p. 231):

Although it is possible to find similarities between the egg-white profiles of *Phaëthon* and some of the Laridae a similar pattern is found in several of the lower orders, for example in some of the herons and ibises. Thus while one may safely assume that the similarity between *Phaëthon* and *Fregata* is the result of relationship it would be rash to ascribe the tropic bird–gull similarities to the same cause without further tests of protein identity.

The pattern of *Pelecanus* resembled that of *Sula bassana* and those of *Ardea* and

Mycteria, *Phalacrocorax* and *Anhinga* had nearly identical patterns. There was considerable variation among the patterns of *Sula*, which seemed to represent species differences. The Pelecaniformes may be polyphyletic but "further evidence on this question is needed" (p. 231).

From a study of cranial kinesis and morphology Simonetta (1963) furnished further evidence for the possible polyphylety of the Pelecaniformes. In his opinion, *Fregata* is closely related to the Diomedidae, but *Phaethon* is an isolated genus of uncertain affinities.

Van Tets (1965) observed the social communication patterns of 15 pelecaniform species and made comparisons with those of other species reported in the literature. These patterns are derived from four main activities: locomotion (pre-take-off and post-landing displays), aggression, nesting, and begging. Although he was cautious about drawing any taxonomic conclusions from his data, he felt that the behavioral evidence best supported Lanham's arrangement (1947). Van Tets also found several behavioral differences between the gannets (*Morus*) and the boobies (*Sula*) that he considered important enough to warrant separation of the two genera. Regarding the nearest relatives of the order, he wrote (p. 75):

The close affinities of the Pelecaniformes to Procellariiformes and the Ciconiiformes are indicated by the mutual displaying of members of a pair facing each other on the nest as occurs not only in the gannets and in a modified form in the frigatebirds but also in the albatrosses, fulmars, and storks. A further resemblance can be noted . . . between the Rattling of the frigate birds and the Clapping displays of albatrosses and storks, between the Stretch display of herons and the Sky-pointing of boobies and the Wing-waving of the Little Pied Cormorant [*Phalacrocorax melanoleucus*], and between the Snap display of herons and the Snap-bowing of the Anhinga and the Gape-bowing of the Little Pied Cormorant. How many of these similarities are due to either homology or analogy still remains to be determined.

Meyerriecks (1966) reviewed Van Tets' work favorably but Nelson (1967) pointed out some apparent errors, particularly in the displays of the Sulidae.

The adaptations for feeding and locomotion in *Anhinga anhinga* and *Phalacrocorax auritus* were carefully analyzed by Owre (1967). The differences in the ecology of these species coupled with associated differences in osteology, myology, and external morphology led him to maintain anhingas and cormorants in separate families.

The Mallophaga of *Phaethon* and *Fregata* are most like those of the Procellariiformes (Timmermann, 1965). The Mallophaga of *Phaethon* and of the Procellariiformes are also related to those of the Charadriiformes. Timmermann concluded that *Phaethon*, *Fregata*, the procellariiforms and the shorebirds (especially the Laridae) are related. The Mallophaga do not suggest a close relationship between the procellariiforms and the other pelecaniforms.

Tyler (1969) was unable to distinguish among the Phaethontidae, Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae, or Anhingidae on the basis of numerous egg shell characteristics that he compared, except that the Pelecanidae have a greater amount of shell nitrogen than the others.

SUMMARY

The taxonomic opinions cited in the preceding review may be summarized as follows:

1) If the Pelecaniformes are considered as a group, most opinions have supported a relationship to the Ciconiiformes, next to the Charadriiformes, Falconiformes

and Procellariiformes and, to a lesser extent, to the Anseriformes. The Sphenisciformes, Gruiformes and Gaviiformes were also mentioned by at least one author.

2) *Fregata* and *Phaethon* are separated from the other pelecaniform birds in a large percentage of the cited papers. *Fregata* has been suggested as a relative of the Charadriiformes, Falconiformes and Procellariiformes. *Phaethon* is most often thought to be allied to the Charadriiformes (especially Laridae) and also to the Procellariiformes.

Our evaluation of the evidence reviewed suggests that the Pelecaniformes are a diverse group but that there is no clear indication that any of the presently included genera are more closely related to the members of some other order than to other pelecaniforms.

THE EGG WHITE PROTEIN EVIDENCE

ORDER PELECANIFORMES

FAMILY PHAETHONTIDAE, Tropicbirds. 3/3, fig. 6.

Species examined: *Phaethon rubricauda*, *aethereus*, *lepturus*.

FAMILY PELECANIDAE, Pelicans. 2/6, fig. 6.

Species examined: *Pelecanus occidentalis*, *onocrotalus*.

FAMILY SULIDAE, Boobies, Gannets. 6/9, fig. 6.

Species examined: *Sula bassana*, *sula*, *nebouxi*, *variegata*, *dactylatra*, *leucogaster*.

FAMILY PHALACROCORACIDAE, Cormorants. 15/30, figs. 6, 7.

Species examined: *Phalacrocorax auritus*, *olivaceus*, *sulcirostris*, *carbo*, *fuscicollis*, *capensis*, *pelagicus*, *urile*, *varius*, *atriceps*, *albiventer*, *melanoleucos*, *africanus*, *niger*, *harrisi*.

FAMILY ANHINGIDAE, Anhingas or Snakebirds. 1/1, fig. 8.

Species examined: *Anhinga anhinga*. (Some authors recognize 3 or 4 species; here we follow Mayr and Amadon, 1951, who placed all anhingas in a single species.)

FAMILY FREGATIDAE, Frigatebirds. 3/5, fig. 7.

Species examined: *Fregata minor*, *aquila*, *magnificens*.

The egg white patterns of the genus *Phalacrocorax* are uniform. The ovalbumin separates in a tripartite arrangement; it is not known whether this is due to the binding of phosphate groups as it is in *Gallus gallus* (see ovalbumin discussion in Materials section). The crescent-shaped bands distinguish cormorants from all other groups with three bands except the Sulidae and Anhingidae. A dense ovomucoid is present cathodal to the ovalbumin. The conalbumins usually migrate anodal to Component 18, but these proteins seem to be quite unstable and only in the freshest material are the bands sharply defined.

The pattern of *Anhinga* matches that of *Phalacrocorax* in the arrangement of the albumins and in details of other components, thus indicating a close relationship to the cormorants.

The patterns of the Sulidae are quite uniform and resemble those of the cormorants. Most patterns of *Sula* have two bands in the ovalbumin region. These bands are crescent-shaped as in *Phalacrocorax* but their relative mobility anodally is slightly less. A third band seems to be masked by the more cathodal ovalbumin component, for in dilute patterns from fresh material three bands can be distinguished. The ovomucoid of *Sula* has a greater anodal mobility than that of *Phalacrocorax*. The conal-

bumins vary in position, being either anodal or cathodal to Component 18. Perhaps this is why the patterns of *Sula*, which appear so different from one another in paper electrophoresis (Sibley, 1960), appear "similar" to one another in starch gel.

Pelecanus agrees with *Sula* in the position of its ovomucoid and Component 18, the latter having a slightly greater anodal mobility than in *Phalacrocorax* and *Anhinga*. *Pelecanus* is also like *Sula* in the arrangement of the ovalbumin. A sharply defined, more anodal component moves ahead of a broader one that in dilute samples appears to be subdivided. The ovalbumin region of *Pelecanus* moves anodally more than that of *Sula* and thus in mobility is more like that of *Phalacrocorax*.

The pattern of *Phaethon* differs from those of the above groups. The ovalbumin region, which has the same mobility as that of *Phalacrocorax*, usually appears as a broad band but in fresh dilute material it can be seen to be composed of two or perhaps three bands. The patterns from older samples do not show this subdivision of the ovalbumin and hence resemble those of the Charadriiformes. The ovomucoid of *Phaethon* migrates more slowly than those of *Sula*, *Phalacrocorax*, *Anhinga*, or *Pelecanus*. Its mobility is the same as that of the ovomucoids in patterns of the Charadriiformes and Procellariiformes. The conalbumins, migrating just anodally from the application point as in other Pelecaniformes, seem to be unstable and cannot be observed in patterns from stale material. This condition is different from that of the typical Charadriiformes in which the conalbumins persist, if only as a smear, in nearly all samples. Like the Charadriiformes *Phaethon* lacks a prealbumin.

The pattern of *Fregata* resembles that of *Phaethon* in all aspects, except that the ovalbumin is apparently not subdivided. Perhaps this is because very fresh material has not been available for study. *Fregata* also possesses a prealbumin.

The patterns of *Phalacrocorax* and *Anhinga* resemble each other most closely. The pattern of *Sula* is most like that of *Pelecanus*, but both genera have similarities to the patterns of *Anhinga* and *Phalacrocorax*. The pattern of *Phaethon* may be a modification of the patterns of the above genera. The pattern of *Phaethon* resembles that of *Fregata*, but the meaning of this similarity is difficult to assess.

CONCLUSIONS

By comparison with most other orders of birds the differences among the egg white protein patterns of the subgroups of the Pelecaniformes are large. However, they can be considered to be modifications of a single ancestral pattern type and the differences may reflect the large genetic gaps which have developed during their long evolutionary history.

In other characters *Phaethon* and *Fregata* seem to be the most aberrant pelecaniform genera. They may be more closely related to the members of some other order but, lacking proof of such a relationship, we propose no modifications of the presently accepted arrangement. Neither do we believe that this question has yet been settled beyond all doubt.

ORDER CICONIIFORMES

Suborder Ardeae

Family Ardeidae, Herons, Bitterns

Family Cochleariidae, Boatbilled-Herons

Suborder Balaenicipites

Family Balaenicipitidae, Whaleheaded Storks

Suborder Ciconiae

Superfamily Scopoidea

Family Scopidae, Hammerheads

Superfamily Ciconioidea

Family Ciconiidae, Storks, Jabirus

Superfamily Threskiornithoidea

Family Threskiornithidae, Ibises, Spoonbills

Suborder Phoenicopteriformes

Family Phoenicopteridae, Flamingos

Wetmore, 1960

INTRODUCTION

The ciconiiforms are typically long-legged, long-necked birds usually dependent to some degree upon an aquatic habitat. All have a desmognathous palate and share a few other characters of uncertain taxonomic significance but the subgroups vary considerably among themselves. The Pelecaniformes and Anseriformes are most frequently suggested as relatives. The Cathartidae repeatedly have been proposed as allies of the storks. *Balaeniceps*, *Scopus* and *Cochlearius* are the principal "problem" genera that have received the attention of many authors.

The flamingos, which seem to share ciconiiform and anseriform characters in a bewildering mosaic, have stimulated the production of a large, complex literature. They will be considered in a separate section, following the review of the other ciconiiforms.

The major taxonomic questions pertaining to the Ciconiiformes may be framed as follows:

- 1) Are the herons, storks and their allies most closely related to the Pelecaniformes, the Anseriformes or to some other order?
- 2) Are the similarities between storks and cathartid vultures due to convergence or to common ancestry?
- 3) Is *Balaeniceps* a heron, a stork or a pelecaniform bird?
- 4) Is *Scopus* a heron or a stork?
- 5) Is *Cochlearius* most closely related to *Balaeniceps*, to *Nycticorax* or to some other genus?
- 6) Are the flamingos most closely related to the ciconiiforms and convergently similar in some characters to the anseriforms or vice versa?

HISTORICAL REVIEW OF THE CLASSIFICATION

A. HERONS, STORKS, IBISES

Nitzsch (1840) placed the herons (including *Cochlearius*) and *Eurypyga* in his "family" Erodii. *Ciconia*, *Anastomus*, *Ibis*, and *Scopus* differ from the "Erodii" in their pterylosis, in his opinion, and were given separate family rank as the Pelargi. A third family, the Hemiglottides, was composed of the ibises and spoonbills and showed similarities to the storks and to the plovers and sandpipers.

The powder-down patches on the lower back of *Balaeniceps* were discovered by A. Bartlett (1860, 1861), who therefore concluded that *Balaeniceps* is more closely allied to the herons than to the storks and pelicans. Bartlett also found the structure of the hind toes and of the viscera (stomach, liver and intestine) to be heron-like. However, Reinhardt (1860, 1862) regarded *Balaeniceps* as most closely allied to *Scopus*. He considered his subfamily containing *Scopus* and *Balaeniceps* to be more closely related to the storks than to the herons.

Parker (1860, 1861) was impressed by the osteological similarities among *Balaeniceps*, *Scopus* and *Cochlearius* and concluded that the three genera are closely related. He also expressed his confidence in the ciconiiform affinities of *Balaeniceps*.

The ciconiiform birds were included in Huxley's Pelargomorphae (1867). He thought that the ibises and spoonbills are most closely related to the flamingos and that the herons and storks are more closely allied to the Pelecaniformes.

Garrod (1873d, 1874a) arranged the cohorts within his order Ciconiiformes in the following sequence: Pelargi (storks), Cathartidae, Herodiones, Steganopodes, Accipitres, indicating his belief in an alliance between the New World vultures and the storks.

Reichenow (1877) thought that *Balaeniceps* is ciconiiform and most closely related to *Scopus* but also bears a relationship to the storks. His diagram of the relationships of the Ciconiiformes shows two main branches stemming from the ibises. One branch leads to the herons, the other to the storks. Though located next to the storks, *Balaeniceps* is pictured as being an offshoot from *Scopus*, which lies off the branch leading to the herons.

The ciconiiform birds were placed between the Steganopodes and the Anseres by P. Sclater (1880) and encompassed the families Ardeidae, Ciconiidae, and Plataleidae. Reichenow's order Gressores (1882) included the Ibisidae (= Threskiornithidae), Ciconidae [sic], Phoenicopteridae, Scopidae, Balaenicipidae, and Ardeidae. Stejneger (1885) recognized the same families but gave superfamily rank to the ibises

and spoonbills within his order Herodii and transferred the flamingos to his order Chenomorphae (= Anseriformes).

Beddard (1884: 552) concluded that *Scopus* is intermediate between the Ciconiidae and Ardeidae. "On myological grounds only it would be difficult to assign it definitely to either group, in fact, the only features in which this genus especially resembles the Herons and differs markedly from the Storks are the form of the syrinx and the air-sacs, while, as already stated, the arrangement of the feather-tracts and the structure of the skeleton are more particularly Stork-like." Beddard (1888a) determined from a diagnosis of the osteological characters of the Ciconiiformes that *Balaeniceps* is a typical stork. He stated that herons, storks, and *Balaeniceps* are extremely similar osteologically, with some herons having stork-like characters and some storks having heron-like characters.

An osteological study convinced Shufeldt (1889b) that the North American species of the subfamily Ardeinae are all closely related. He recognized only *Nycticorax* for the night-herons and *Ardea* for the remaining species. Presumably a single genus of bitterns, *Botaurus* (including *Ixobrychus*), would be placed in an adjacent subfamily.

The arrangement of secondary coverts in the Ardeidae is most like that of the Accipitres, excluding *Sagittarius* and the Cathartidae (Goodchild, 1886). *Leptoptilos*, however, is like the Cathartidae in this character. *Platalea* and *Ibis* (= *Threskiornis*) differ little from *Ciconia*, but the arrangement of these feathers in *Tantalus* (= *Ibis*) is charadriiform.

Fürbringer (1888) gave separate family rank to *Balaeniceps* and *Scopus* but assigned *Cochlearius* to the Ardeidae. The ciconiiform birds formed the "gens Pelargo-Herodii" in his system and he thought them to be related to the peleaniform and falconiform birds as well as to the flamingos.

Within an Ardeino-Anserine order Seebohm (1889) formed a suborder Plataleae for the ibises and spoonbills and another, Herodiones, for the herons and storks. He placed the two suborders between the Phoenicopterii and the Steganopodes. In his opinion, *Balaeniceps* and *Scopus* belong to the Ciconiidae, *Cochlearius* to the Ardeidae. In his 1890 classification the Plataleae and Herodiones were still recognized, but they and the Steganopodes were placed in an order separate from that of the flamingos and waterfowl. In 1895 Seebohm shifted hierarchies again. The Herodiones, Anseres and Steganopodes were treated as suborders of the Ciconiiformes, with the Ibididae, Scopidae, Ardeidae and Ciconiidae as families in the Herodiones.

Gadow (1893) defined an order Ciconiiformes that included the suborders Steganopodes, Ardeae, Ciconiae, and Phoenicopterii. He found characters which seemed to ally distantly the Ciconiiformes to the Anseriformes and Falconiformes. He concluded that *Cochlearius* and *Balaeniceps* belong in the Ardeidae but established a separate family within his Ardeae for *Scopus*.

The order Pelargiformes of Sharpe (1891) contained the suborders Ardeae, Ciconii, Balaenicipetides, Scopi, and Plataleae. The latter group had two families, the Plataleidae (spoonbills) and Ibididae (ibises). Sharpe's diagrams indicate that he thought the ciconiiform birds to be most closely allied to the flamingos and waterfowl on one hand and to the New World vultures on the other.

Sharpe (1898) required two orders for the storks and their allies. The order Plataleae included the Ibididae (ibises) and Plataleidae (spoonbills). The Herodiones included the Ardeidae, Balaenicipitidae [sic], Scopidae, and Ciconiidae. *Cancroma* (= *Cochlearius*) was placed between *Nycticorax* and *Gorsachius* in the Ardeidae.

Beddard (1898a) reviewed the characters and the taxonomic history of the ciconiiforms (Herodiones) and recognized as families the Scopidae, Ciconiidae, Ardeidae, Balaenicipidae, Plataleidae and Phoenicopteridae. He discussed (p. 442-43) the

assertion "that there are likenesses between the Herodiones and the accipitrine birds" which "reduces itself to a comparison between the Herodiones . . . and the Cathartidae and *Serpentarius*. . . ." Beddard pointed to two similarities between ciconiiforms and "these lower accipitrines," namely, the coiling pattern of the intestines and the lack of a syrinx in storks and cathartid vultures. The first of these he ascribed to convergence and the second "point of resemblance rests . . . upon mere negativity" (p. 443). He stated that the syringeal loss in the two groups had occurred in different ways and that "there is . . . as much to be said for a derivation of the Accipitres from the crane as from the pelargine stock. . . ."

Proposed alliances of the Ciconiiformes to either the Pelecaniformes or the Falconiformes were viewed skeptically by Shufeldt (1901d). He believed that the ciconiiform birds are linked to the waterfowl through the spoonbills and the flamingos. Of the Ciconiiformes the Ardeidae were to him the most distinctive group, and the storks and ibises seemed closely allied through *Mycteria americana*.

After a thorough study of the anatomy of *Balaeniceps*, Mitchell (1913) doubted that anatomical characters were adequately understood as indicators of phyletic relationships. As a practical solution, he weighted all characters equally and grouped *Balaeniceps* with the storks, ibises and *Scopus* in the suborder Ciconiae, while placing the herons in the subfamily Ardeae. He emphasized that this was a temporary phenetic classification, not an expression of phylogenetic relationships.

Chandler (1916) found enough differences in feather structure between the storks and ibises on the one hand and the herons on the other to warrant placing them in separate suborders within his Ciconiiformes, which also contained the Steganopodes and the Phoenicopterii. He concluded (p. 324): "The Ardeae, or at least the Ardeidae, seem to form an end branch from the ciconiid stem, being comparatively more specialized than the Ciconiae, and apparently not giving rise to any other orders or suborders. *Eurypyga*, and to a lesser extent, *Cariama*, . . . have a feather structure which is so heron-like that the possibility of their inclusion in the Ardeae is strongly suggested. *Cursorius* likewise has a feather structure which strongly argues for its inclusion in this group."

The ciconiiform birds are apparently most closely related to the Pelecaniformes and Falconiformes, according to E. Stresemann (1927-34). Although he formed separate monotypic families for *Balaeniceps* and *Scopus* within his order Gressores, he believed that they were more closely allied to the storks than to the herons. He assigned *Cochlearius* to the Ardeidae.

After a study of the skulls of young and adult specimens of *Balaeniceps*, Böhm (1930) concluded that *Balaeniceps* is a typical stork, converging toward *Cochlearius* in the shape of the bill. He evaluated the resemblance of *Balaeniceps* to *Scopus* as superficial, asserting that they and *Cochlearius* share these osteological similarities.

The trematodes of herons and storks are markedly different, those of the herons suggesting a relationship to the Falconiformes (Szidat, 1942). However, parasites from genera that are possibly intermediate between herons and storks were not examined.

Using the evidence from the Mallophaga, Hopkins (1942) attempted to clarify the relationships of *Scopus*. He found two genera on *Scopus* (*Quadriceps* and *Austromenopon*) that are found also on Charadriiformes. (Timmermann, 1963, reported *Austromenopon* from the Procellariiformes as well.) *Scopus* shares only one genus, *Colpocephalum*, with the Ciconiidae, Phoenicopteridae, and Anatidae. Hopkins suggested that 1) *Scopus* is a charadriiform bird which had secondarily picked up *Colpocephalum* from a stork, or 2) the Ciconiiformes and Charadriiformes had a common ancestor and that *Scopus* is an early offshoot from the charadriiform branch of this stem.

Clay (1950), who also studied the Mallophaga, noted that of nine genera found on Ciconiiformes three are common to the Ardeidae, Ciconiidae, and Threskiornithidae (*Colpocephalum*, *Ciconiphilus*, *Ardeicola*), but only *Ciconiphilus* has been found on *Balaeniceps*. She also wrote (p. 435):

One genus (*Ciconiphilus*) found on the Ciconiiformes is also found on *Cygnus* (Swans: Anseriformes) and another (*Ibidoecus*) characteristic of the Threskiornithoidae (Ibises) is also found on *Aramus scolopaceus* (Limpkin: Gruiformes); a third genus (*Laemobothrion*) found on some of the Threskiornithoidae is again found on *Aramus*, but this genus has a wide distribution with species on the Rallidae (Rails), Psophiidae (Trumpeters), *Opisthocomus* (Hoatzin) and less closely related species on the Falconiformes (Birds of Prey). The distribution of these genera suggests that *Ciconiphilus* may be a straggler on the swans from the Ciconiiformes, *Ibidoecus* a straggler on *Aramus* from the Threskiornithoidae and *Laemobothrion* a straggler on this latter superfamily from the Rallidae.

Mayr and Amadon (1951) included *Cochlearius* in the Ardeidae and *Balaeniceps* in the Ciconiidae. They felt that the Ciconiiformes may be related to the flamingos.

W. Bock (1956) revised the classification of the Ardeidae using a reevaluation of traditional taxonomic characters. The most useful characters in assessing relationships were the powder-down patches, structure of plumes, general proportions, color pattern, and nesting habits. Bock's classification follows:

Family Ardeidae

Subfamily Botaurinae

Botaurus stellaris, *poiciloptilus*, *lentiginosus*, *pinnatus*
Ixobrychus exilis, *minutus*, *sinensis*, *involucris*, *eurhythmus*, *cinnamomeus*,
sturmi, *flavicollis*

Subfamily Ardeinae

Tribe Tigriornithini

Zonerodius heliosylus
Tigriornis leucolophus
Tigrisoma lineatum, *salmoni*, *mexicanum*
Zebrilus undulatus

Tribe Nycticoracini

Gorsachius goisagi, *melanolophus*, *magnificus*, *leuconotus*
Nycticorax nycticorax, *caledonicus*, *pileatus*, *violaceus*, *sibilator*
Cochlearius cochlearius

Tribe Ardeini

Ardeola ralloides, *idaea*, *grayii*, *bacchus*, *speciosa*, *rufiventris*, *ibis*
Butorides virescens, *sundevalli*, *striatus*
Hydranassa picata, *ardesiaca*, *caerulea*, *tricolor*, *rufescens*
Egretta sacra, *eulophotes*, *thula*, *gularis*, *dimorpha*, *garzetta*, *intermedia*, *alba*
Ardea purpurea, *novaehollandiae*, *pacifica*, *cinerea*, *herodias*, *occidentalis*,
cocoi, *melanocephala*, *humboldti*, *goliath*, *imperialis*, *sumatrana*
Agamia agami

The genera recognized by Peters (1931) and synonymized by Bock are as follows: *Bubulcus* and *Erythrocnus* were merged with *Ardeola*; *Calherodias* and *Oronassa* with *Gorsachius*; *Casmerodius*, *Demigretta*, *Leucophoyx*, and *Mesophoyx* with *Egretta*; *Dichromanassa*, *Florida*, *Melanophoyx*, and *Notophoyx picata* with *Hydra-*

nassa; *Dupetor* with *Ixobrychus*; *Heterocnus* with *Tigrisoma*; *Pilherodius*, *Syrigma*, and *Nyctanassa* with *Nycticorax*; *Notophoxyx novaehollandiae* with *Ardea*.

Adams (1955) compared the skeletons of *Nycticorax* and *Nyctanassa* and concluded that they should be retained as separate genera.

Humphrey and Parkes (1963) disagreed with Bock's proposal to merge *Syrigma* with *Nycticorax*. From field studies of behavior and voice and an evaluation of molts, juvenal plumage, and the structure of the cervical vertebrae, they concluded that *Syrigma* belongs in the tribe Ardeini as defined by Bock.

Eisenmann (1965) clarified the species boundaries in the genus *Tigrisoma*, which should include three species, namely, *lineatum*, *fasciatum* (including *salmoni*), and *mexicanum*.

Balaeniceps rex differs from the herons and storks and resembles members of the Pelecaniformes in a number of osteological characters. According to Cottam (1957), "This species could occupy a monotypic family in the order Pelecaniformes, possibly near the Pelecanidae" (p. 70). The main points of similarity are the following:

1) *Balaeniceps* has a well-developed hook at the tip of the premaxilla like *Pelecanus*, *Phalacrocorax*, *Fregata*, and the newly hatched chicks of *Sula*. A conspicuous groove running from the anterior edge of the nostril, flanking the culmen, to the cutting edge of the premaxilla beside the terminal hook is shared by *Balaeniceps*, *Pelecanus*, *Sula*, *Phalacrocorax* and *Fregata*.

2) The nasal septum is ossified in *Balaeniceps*, the Pelecani, and the Fregatae; in *Balaeniceps*, as in *Pelecanus*, the external nares are above the internal nares, with the nasal cavity situated ventrally between them.

3) The palatine bones of *Balaeniceps* are ankylosed along the midline, posterior to the internal nares. There is a broad ventral ridge above the suture, along side of which lie depressions for the attachment of the pterygoid musculature. This condition is quite similar to that found in *Sula*, *Phalacrocorax*, and *Pelecanus* and also resembles that of *Fregata*.

4) *Balaeniceps*, the Pelecani, and *Fregata* each have a large lachrymal which meets the quadratojugal bar. In *Balaeniceps*, complete occlusion of the antorbital vacuity is achieved by fusion of the lachrymal with the maxilla; in the Pelecani, particularly *Sula*, and in the Fregatae there is a tendency toward reduction of the antorbital cavity.

5) While the jaw articulation in *Balaeniceps* resembles that of the Ardeidae in some respects, it agrees with that of the Fregatae and Pelecani in those aspects differing from the ciconiiform condition.

6) The hypocleideum of the furcula of *Balaeniceps* is fused to the keel of the sternum, as it is in *Fregata* and many specimens of *Pelecanus*.

7) The form of the first metatarsal in *Balaeniceps* and the presumed function of the first toe seems more like those of *Pelecanus* than like those of any of the ciconiiform birds.

Wetmore (1960) admitted that *Cochlearius* superficially resembles the black-crowned night heron (*Nycticorax nycticorax*) but emphasized that *Cochlearius* differs from the typical herons in numerous characters of the skull. He also pointed out that the "eyes, wood brown by day, at night reflect the jacklight with a faint orange sheen, which I have not observed in other herons" (p. 10), and concluded that "from long acquaintance I regard their characters . . . sufficient to maintain a separate family status."

Meyerriicks (1960) published a detailed study of the breeding behavior of four North American species of herons, with comparisons to six others. Although stating that this investigation was not comprehensive enough to permit taxonomic specula-

tion, he felt that such speculation should include the evolution of ardeid social behavior, which he summarized (p. 142) as follows:

The probable course of social evolution in herons has been from the primitive solitary status exemplified by *Botaurus*, through a transitory semisocial phase (*Butorides* and *Ixobrychus*), to extreme, year around sociality, represented by *Leucophoyx*, *Bubulcus*, and *Nycticorax*. The night herons (*Nycticorax* and *Nyctanassa*) must have evolved their present highly social structure independently of such species as [*Egretta*] *thula* and [*Hydranassa*] *rufescens*, because they differ in numerous other respects, both behavioral and structural.

The Ciconiiformes of Verheyen (1959a, 1960g) contained the suborders Ardeae, Scopi, Ciconiae, and Balaenicipites. In his opinion, the Ciconiae are related to the Phoenicopteriformes and Charadriiformes through the ibises and spoonbills. *Balaeniceps* and some of the Ardeae were thought by Verheyen to link the order with the Pelecaniformes. *Cochlearius* was given only tribal rank within the Ardeidae. In his 1961 classification Verheyen limited his Ciconiiformes by including only the Scopidae, Ciconiidae, and Threskiornithidae. He placed *Balaeniceps* and the herons in the adjacent order Ardeiformes, and, following Wetmore (1960), raised *Cochlearius* to family rank.

Using paper electrophoresis Sibley (1960) examined the egg white proteins of 17 species of herons, five ibises and spoonbills, one stork and one flamingo. The classification proposed by W. Bock (1956) for the herons seemed to be supported by the variation within the Ardeidae; the herons, ibises, storks and flamingos showed more similarities to one another than to any other order. The pattern of *Mycteria* "shows affinities to the herons and the ibises and is similar to *Pelecanus*." The heron patterns also contained "resemblances to the loons, some Pelecaniformes, and some Charadriiformes." The possible relationship to the diurnal birds of prey was neither opposed nor strongly supported by the egg white comparisons.

Kahl and Peacock (1963) described the bill-snap reflex of the wood stork (*Mycteria americana*). This is a tacto-locating method for seizing prey in turbid water. Kahl (1966a) found that this method was used also by *Leptoptilos cruminiferus* and *Ibis ibis* when feeding in muddy water.

Kahl (1963) observed that storks, when overheated, react by rapid panting and excreting feces on their legs (= "urohidrosis"). He suggested that the latter is a behavioral mechanism for increasing heat loss by evaporation of the liquid excreta. Since this behavior is found widely in ciconiids, but not in other groups (except the Cathartidae), Kahl reasoned that it arose early in the evolution of storks and might appear in other ciconiiform genera if they are closely related to storks. When he performed heat stress experiments on *Scopus* and *Balaeniceps*, Kahl (1967a) found that *Scopus* reacted by rapid continuous panting with over a ten-fold increase in breathing rate, but did not excrete on its legs. *Balaeniceps* reacted by intermittently fluttering the gular region, like herons and pelicans do. Kahl concluded that neither species seems closely related to the storks, but that more knowledge of the sexual displays of these birds is needed.

Kahl (1967b) found additional behavioral differences between *Scopus* and the storks. *Scopus* flies buoyantly unlike either storks or herons, but like storks it does occasionally soar. On the ground *Scopus* does not rest by sitting on its tarsi as storks often do. When resting in trees its legs are folded under the body and the breast touches the perch, a posture unlike those of storks. *Scopus* was not seen to use the bill-snap method in feeding, but did employ foot-stirring like that of herons. The bill-clattering displays of storks and the stretch displays of herons have no counterparts

in *Scopus* and it does not have the habit of exchanging sticks during nest building as in many other Ciconiiformes.

Kahl (1964, 1966b) has also studied the ecology and breeding biology of *Mycteria* and *Leptoptilos*. The possible functions of the "spread-wing" postures of the storks were studied by Kahl (1971). He came to no taxonomic conclusions but did suggest that the presence of "urohidrosis" in storks, New World vultures and at least one cormorant might indicate relationships.

Working mainly from osteological characters, Ligon (1967) emphasized the "extreme anatomical dissimilarities" between the Ardeidae and Ciconiidae and placed them in separate orders. Like several earlier authors he declared the New World vultures (Cathartidae) to be related to the storks and included them in the same order. Unfortunately he did not compare any other ciconiiform groups.

The relationships of *Cochlearius* were reexamined by Cracraft (1967). Of 31 characters of the postcranial skeleton *Nyctanassa* differed from *Nycticorax* in eight, and *Cochlearius* differed from *Nycticorax* in ten. The genera *Pilherodius* and *Gorsachius* differed more widely. Cracraft felt that the complex of skull characters in which *Cochlearius* differs from typical herons probably evolved rapidly and recently. If one weights these features plus the presence of four patches of powder down most heavily, then tribal status for *Cochlearius* may be maintained. If, however, most importance is given to the postcranial osteology, then *Cochlearius* may be placed in the tribe Nycticoracini.

Curry-Lindahl (1968, 1971) compared the ritualized display movements of ardeids at their breeding colonies and also observed feeding techniques and other behavior patterns. His data largely corroborated the relationships proposed by W. Bock (1956), with the exception of the following points:

- 1) *Ixobrychus sturmi* is transferred to the monotypic genus *Ardeirallus*.
- 2) *Nycticorax pileatus* is transferred to the monotypic genus *Pilherodius*.
- 3) *Egretta alba* is placed in *Ardea*.
- 4) *Butorides virescens* and *striatus* probably should be regarded as races of a single species, as should *Egretta garzetta* and *thula* and *Ardea cinerea* and *herodias*. [The merger of *A. cinerea* and *herodias* was also made by Parkes, 1955.]

The appendicular musculature of 21 ciconiiform genera, representing all families except the Scopidae, were examined by Vanden Berge (1970). Generally he found a lack of consistency in the muscle patterns that was difficult to interpret taxonomically. He thought that the ciconiiform birds, flamingos included, were more similar to one another than any one was to another avian order. He rejected Ligon's (1967) decision to split the order, but agreed with W. Bock (1956) and Cracraft (1967) in considering *Cochlearius* most similar to the night herons (*Nycticorax*).

Sibley, Corbin and Haavie (1969) compared the electrophoretic patterns of the hemoglobins of six ciconiiforms, two flamingos and six anseriforms, including two anhimids. There was considerable variation among these patterns but many points of similarity as well and the authors declined to draw any conclusions about relationships.

SUMMARY FOR CICONIAE. In addition to the Anseriformes the Pelecaniformes and Falconiformes (especially the Cathartidae) have been proposed as the nearest relatives of the Ciconiiformes. A majority of workers have found similarities among the storks, ibises, and spoonbills, and have tended to emphasize the differences between the herons and storks. That *Cochlearius* is ciconiiform has not been questioned, but whether it deserves family rank has been disputed. Most of those placing it in the Ardeidae have considered it allied to the night herons (*Nycticorax*).

Scopus has generally been considered to be ciconiiform, but an alliance to the

Charadriiformes has also been suggested. Among the Ciconiiformes, *Balaeniceps* and the Ciconiidae have most frequently been proposed as the nearest relatives of *Scopus*.

Balaeniceps likewise has been thought to be ciconiiform, with its allies being *Scopus* or the Ciconiidae. Some authors have maintained that *Balaeniceps* is pelecaniform.

An alliance between the ibises and the shorebirds has been postulated occasionally, and the gruiform genera *Eurypyga*, *Cariama*, and *Aramus* have been considered ciconiiforms by at least one author.

B. FLAMINGOS

One of the most controversial and long-standing problems in avian systematics has been the relationships of the flamingos. Because the taxonomic literature on the group is unusually extensive and complex, we will discuss it separately here rather than combine it with that on the other ciconiiforms.

Sibley, Corbin and Haavie (1969) presented a review of the literature bearing on the flamingo problem. Here we will cite primarily those studies that directly concern the question of their allocation to one or another of the orders of birds.

Nitzsch (1840) regarded the flamingos as a distinct "family", the Odontoglossae. He found the pterylosis to be most similar to that of *Ciconia* and *Tantalus* (= *Ibis*). G. Gray (1849) placed the Phoenicopteridae next to the Anatidae in his order Anseres, which contained all birds with palmately webbed feet. Although it is now clear that the palmate condition of avian feet has evolved independently more than once, the debate concerning the herons vs. geese as the closest relatives of the flamingos dates back to the beginning of the "modern" era in avian systematics—more than a century ago.

Huxley (1867: 460) concluded that "the genus *Phoenicopterus* is so completely intermediate between the anserine birds on the one side, and the storks and herons on the other, that it can be ranged with neither of these groups, but must stand as the type of a division by itself." Huxley thus became one of the first to adopt an essentially neutral position in the herons vs. geese argument, a position still espoused by many who, like Huxley, find the conflicting evidence impossible to evaluate.

Mainly on the basis of the pelvic muscle formula, the presence of caeca and an aftershaft, and the bicarotid condition, Garrod (1873d, 1874a) placed *Phoenicopterus*, along with *Burhinus*, *Sagittarius*, and *Cariama*, in the Otididae of his order Galliformes. This conclusion of Garrod demonstrates the nonsense that can emerge from blind dependence upon a few characters that have been accepted in advance as definitive.

P. Sclater (1880) considered the flamingos to represent an order intermediate between the ciconiiform and anseriform birds, but Reichenow (1882) included the flamingos as a family within his order Gressores (= Ciconiiformes) with no obvious ties to the waterfowl. Stejneger (1885) placed the flamingos in his order Chenomorphae (= Anseriformes), but agreed that they also are related to the herons. Among the characters he mentioned as being shared by flamingos and waterfowl are the elongated nasals and lachrymals, the narrow frontal bones, the presence of grooves for the supraorbital glands, the presence of basipterygoid processes, the shape of the furcula and scapulae, the lamellate beak, palmate feet, and the presence of 14 tail feathers.

Fürbringer (1888) remained unconvinced of a relationship between the flamingos and waterfowl. He placed the flamingos in a "gens" next to the Pelargo-Herodii

in his suborder Ciconiiformes. This suborder also contained the pelecaniiforms and falconiforms.

From an anatomical study of five storks, seven species of waterfowl, and *Phoenicopterus ruber*, Weldon (1883: 65) concluded that "while the skull and larynx of *Phoenicopterus*, together with its webbed feet and the characters of its bill, undoubtedly connect it with the Lamellirostres [= Anseriformes], yet the rest of its organs—its air-cells, its muscles, its alimentary canal, its vertebral column, and the characters of its wing bones—show close relationship with the Storks." He preferred to recognize a separate order for the flamingos, as Huxley (1867) had done.

The pterylography, osteology, myology, and internal anatomy of *Phoenicopterus* convinced Gadow (1877) that it is ciconiiform and probably most closely allied to the storks and spoonbills. Later he (1889) pointed out that on the basis of the pattern of intestinal convolutions, the flamingos are closely allied to the Ciconiae. They share no features in common with the waterfowl except small functional caeca. In his definitive system of 1893 Gadow still kept the flamingos as a suborder within his Ciconiiformes, but admitted that they have several important points of similarity to the Anseriformes and concluded that the two orders were linked by the Anhimidae and Phoenicopteridae.

Seebohm (1889) concluded from a study of osteology that the flamingos are intermediate between ducks and herons and closely related to both the Palamedeae (= Anhimidae) and Plataleae (= Threskiornithidae). He ranked these groups as suborders within a large "Ardeino-Anserine" order. Soon Seebohm (1890) changed his opinion and recognized an order Lamellirostres, containing the suborders Phoenicopterii, Anseres, and Palamedeae (= Anhimae). This order was placed next to the order Pelecano-Herodiones. A few years later (1895) Seebohm's thoughts changed once again. This time he erected an order Ciconiiformes with suborders Herodiones, Anseres, and Steganopodes. Within the Anseres he recognized the families Anatidae, Phoenicopteridae, and Palamedeidae.

The flamingos have an arrangement of their secondary wing coverts similar to that of the spoonbills and storks, except *Leptoptilos* (Goodchild, 1891). In this character Goodchild thought that herons and bitterns resemble the waterfowl and the birds of prey. Wray (1887) pointed out that most birds have six flight feathers originating on the metacarpus, but that flamingos, storks, and grebes have seven. Thus these three groups are the only birds possessing 12 primaries. W. D. Miller (1924a: 317) has shown that these three groups have 11 primaries plus the remicle.

Parker (1889a) observed that in the carpals, metacarpals, and phalanges, flamingos are more similar to ibises than to geese.

At first, Shufeldt (1889c) decided that the flamingos were most like the ibises in their osteology, but later (1901e) came to believe that their affinities lie equally with the waterfowl and the Ciconiiformes and proposed placing them in a separate order, the Odontoglossae. The skeletal characters of flamingos, in his opinion, are most similar to those of geese on one hand and on the other to those of the spoonbills, ibises, and storks.

A neutral position was adopted by Sharpe (1891) by giving ordinal rank to the flamingos between his orders Pelargiformes (= Ciconiiformes) and Anseriformes.

Beddard (1898a) reviewed and evaluated the anatomical evidence available to him and concluded that the flamingos are related to the ciconiiforms and that resemblances to the ducks are merely superficial. He placed the Phoenicopteridae in his order Herodiones (= Ciconiiformes).

Mitchell (1901a) concurred with the results of previous studies on the intestinal tract, noting that *Phoenicopterus* was most like *Platalea* in this respect. The only point of similarity to the waterfowl is the presence of a well-developed caecum.

Chandler (1916) thought that four characteristics in the structure of flamingo feathers are like those of the Anseriformes and unlike those of the Ciconiiformes. They are: 1) shape and size of barbules; 2) the form of ventral "teeth" on the proximal and distal barbules; 3) the form of the ventral and dorsal "cilia" on the distal barbules; 4) the presence and form of the ventral barbicels of the outer proximal barbs.

Ordinal status for the flamingos, next to his Gressores (Ciconiiformes), was retained by E. Stresemann (1927-34). He considered flamingos to be "aberrant storks" and attributed the similarities with the waterfowl to convergence. Wetmore (1930, 1934, 1940, 1951) and Peters (1931) placed the flamingos in a suborder of their Ciconiiformes.

According to Howard (1950), the Upper Cretaceous *Parascaniornis* and lower Paleocene *Scaniornis* show evidence of relationships to both herons and flamingos. She considered the Lower Cretaceous genus *Gallornis* to be anseriform, but the material (the proximal portion of a femur and a scrap of humerus) is too fragmentary to offer solid clues to relationships. In 1955 Howard described *Telmabates antiquus* based on a fairly complete postcranial skeleton (lower Eocene; Argentina) and erected for it a new family, *Telmabatidae*, which she thought was ancestral to the flamingos. In her opinion, *Telmabates* resembles the Anseriformes and the fossil flamingo genus *Palaelodus*. She suggested that a separate order be recognized for the *Telmabatidae*, *Palaelodidae*, and *Phoenicopteridae*.

Berlioz (1950) placed the *Phoenicopteridae* in a suborder within his Anseriformes. Mayr and Amadon (1951) considered the conflicting evidence for the relationships of the flamingos, and put them in a separate order between the Ciconiiformes and Anseriformes, noting that "they may be related to both" (p. 7).

The great length of the intestine of flamingos is probably an adaptation to their feeding niche and the occurrence of well-developed caeca in flamingos and waterfowl may be due to convergence (Ridley, 1954).

Glenny (1945, 1953a, 1955) determined that all Anseriformes and most Ciconiiformes have the bicarotid (A-1) arrangement of arteries in the neck region. Some Ardeidae show the B-1 condition in which a single carotid artery enters the hypapophyseal canal, but it is supplied by paired vessels of equal size from both left and right common carotids. *Balaeniceps* has the B-4-s condition in which the right carotid alone enters the hypapophyseal canal. This condition is unique among Ciconiiformes and, in Glenny's opinion, supports the allocation of *Balaeniceps* to a monotypic family. *Botaurus lentiginosus*, *Ardeola speciosa*, and the flamingos have the B-2-s condition. Glenny thought this condition was derived from the B-1 by a reduction in size of the left common carotid, and interpreted it as indicating a relationship between the flamingos and Ciconiiformes. The character seems to be of questionable value in this situation because of its variability within the Ardeidae. For example, *Ardea herodias* has both A-1 and B-1 conditions, and *Botaurus lentiginosus* has both B-1 and B-2-s. Furthermore, in Glenny's phylogeny the B-2-s pattern is derived from the A-1 through the B-1 condition. Hence the flamingos during their long history could have evolved their B-2-s pattern from the basic A-1 arrangement of either the Ciconiiformes or the Anseriformes.

Jenkin's (1957) report on the feeding mechanisms of flamingos pointed out that the shape of the bill, size of the jaws, and configuration of the joints of the mandibles are correlated with the pumping and filter mechanisms of feeding. The filtering apparatus of flamingos seems to be more specialized than that of the waterfowl or the stork *Anastomus*, although, in Jenkin's opinion, both these birds received it from a common ancestor. The bend in the bill of flamingos probably developed

later in evolution, as it does in ontogeny. The straight, goose-like bill of the hatchling flamingo may seem to support these opinions, but the young of the ciconiiform birds with specialized bills, such as spoonbills, also are hatched with straight bills like those of flamingo chicks.

The evidence from the Mallophaga was presented by Hopkins (1942, 1949), Clay (1950, 1957), and Rothschild and Clay (1952), who concluded that it supports a flamingo-anseriform relationship. The flamingos are parasitized by three genera of feather lice (*Anaticola*, *Anatoecus*, and *Trinoton*), which are found elsewhere only on the Anseriformes. The Ciconiiformes are parasitized by different genera than those found on the flamingos and Anseriformes. The flamingos share one genus, *Colpocephalum*, with both orders, but this genus is widespread on other avian groups as well.

Both Mayr (1957) and the parasitologist von Keler (1957) argued that the occurrence of similar feather lice on the flamingos and waterfowl is probably due to a rather recent transfer from the latter to the former group. E. Stresemann (1959) concurred with this point of view and reaffirmed his belief that the flamingos are most closely allied to the Ciconiiformes. Ash (1960) stressed that Mallophaga are poorly known systematically as well as ecologically.

Baer (1957) found that the cestode parasites of flamingos are most like those of the Charadriiformes, thus adding further confusion to the meaning of the evidence from parasites.

Consistent differences between the Ciconiiformes and Anseriformes in the paper electrophoretic patterns of their egg white proteins were demonstrated by Sibley (1960). In a series of comparisons carried out for varying periods of electrophoretic separation, the pattern of the flamingo *Phoeniconaias minor* consistently resembled that of the heron *Ardea herodias* more than it did that of the duck *Anas georgica*. The similarity extended to other Ciconiiformes (e.g., *Mycteria*) as well, and Sibley concluded that the flamingos are related more closely to the Ciconiiformes than to the Anseriformes.

Verheyen (1959a, 1960g, 1961) found many characters suggesting an alliance between the flamingos and both the Ciconiiformes and the Anseriformes. In his classification he gave them ordinal rank between these two orders.

Although Wetmore (1956: 3; 1960: 10) admitted that the flamingos resemble both the Anseriformes and the Ciconiiformes, he placed them as a suborder within the latter group because he emphasized the importance of the fossil genera *Palaelodus* and *Elornis* (upper Eocene—Miocene; western Europe).

The carotenoid pigment canthaxanthin was found in the feathers of all species of flamingos, the scarlet ibis (*Guara rubra*), and the roseate spoonbill (*Platalea ajaja*) by Fox (1962a-c), Fox and Hopkins (1966a,b), Fox, Hopkins and Zilvermit (1965) and Fox, Smith, and Wolfson (1967). Brush (1967), however, found this pigment in the scarlet tanager (*Piranga olivacea*), which limited its utility as a taxonomic character. It is possible that the synthesis of canthaxanthin from its precursor beta-carotene is mediated by similar enzymes in flamingos and ciconiiformes, and that the homologous enzymes in *Piranga* may differ significantly. However, until this is demonstrated, the character must be regarded as unreliable.

Mainardi (1962a) prepared antisera against the red blood cells of a flamingo (*Phoenicopterus ruber*), a stork (*Ciconia ciconia*), a heron (*Ardea cinerea*), an ibis (*Threskiornis aethiopica*), and three species of waterfowl (*Anser anser*, *Anas platyrhynchos*, *Cairina moschata*). Data derived from the heterologous antigen-antibody reactions in all combinations led Mainardi to conclude that the flamingos are equally distant from the Ciconiiformes and the Anseriformes, and thus the three groups are

related. In 1963 he proposed a phylogenetic tree, based on immunological and fossil evidence, in which the waterfowl branched first from a common stem and later the two branches of the flamingos and ciconiiformes diverged.

Sibley, Corbin and Haavie (1969) reviewed the literature on the structure, fossil record, behavior, parasites, life history and proteins of flamingos and concluded that most evidence was conflicting and difficult to interpret. They presented new data from comparative studies of the hemoglobins and egg white proteins, which led them to agree with Mainardi (1963). They recommended that the flamingos be placed in a suborder, Phoenicopterii, in the order Ciconiiformes and that, in a linear list, the Ciconiiformes and Anseriformes be placed adjacent to one another as in the classification of Wetmore (1960).

The starch gel electrophoretic patterns of the hemoglobins of the flamingos *Phoenicopus ruber* and *Phoeniconaias minor* were examined and compared with those of other groups of birds (Sibley, Corbin and Haavie, 1969, and unpublished data). The patterns of the flamingos have at least four components each and resemble those of some ciconiiforms (e.g., *Mycteria*), the boobies (*Sula*), screamers (*Anhima*, *Chauna*), and some anseriforms (e.g., *Cereopsis*). Although the starch gel electrophoretic evidence is ambiguous, the tryptic peptides of hemoglobins (Sibley, Corbin, and Haavie, 1969) indicate greater similarity between the flamingos and ciconiiforms than between flamingos and anseriforms.

SUMMARY FOR PHOENICOPTERI. Almost without exception the flamingos have been considered to be related either to the Ciconiiformes or the Anseriformes or to both. The morphological evidence has been interpreted in all three ways depending upon which characters were weighted most heavily. The fossil record indicates that flamingos are of considerable antiquity, and fossils have been interpreted as showing an alliance to both the herons and waterfowl. The flamingos and waterfowl harbor similar Mallophaga but this condition is interpreted in opposite ways by different authorities. The immunological and previous biochemical evidence suggest that flamingos are closer to herons but that all three groups are related.

THE EGG WHITE PROTEIN EVIDENCE

ORDER CICONIIFORMES

FAMILY ARDEIDAE, Herons, Bitterns. 32/64, figs. 7-9.

Species examined (nomenclature follows W. Bock, 1956): *Botaurus stellaris*; *Ixobrychus exilis*, *minutus*, *sinensis*, *eurhythmus*, *cinnamomeus*; *Tigrisoma mexicanum*; *Nycticorax nycticorax*, *caledonicus*; *Cochlearius cochlearius*; *Ardeola ralloides*, *rufiventris*, *ibis*; *Butorides virescens*, *striatus*; *Hydranassa tricolor*, *rufescens*; *Egretta thula*, *gularis*, *garzetta*, *intermedia*, *alba*; *Ardea purpurea*, *novaehollandiae*, *pacifica*, *cinerea*, *herodias*, *cocoi*, *melanocephala*, *goliath*, *sumatrana*; *Agamia agami*.

FAMILY BALAENICIPITIDAE, Whale-headed Stork. 0/1.

FAMILY SCOPIDAE, Hammerhead. 1/1, fig. 9.

Species examined: *Scopus umbretta*.

FAMILY CICONIIDAE, Storks. 7/17, fig. 9.

Species examined: *Mycteria americana*; *Ibis leucocephalus*, *cinereus*; *Anastomus oscitans*; *Ciconia ciconia*, *nigra*; *Leptoptilos javanicus*.

FAMILY THRESKIORNITHIDAE, Ibises, Spoonbills. 12/28, figs. 9, 10.

Species examined: *Threskiornis aethiopica*, *melanocephala*, *spinicollis*; *Hage-*

dashia hagedash; *Theristicus caudatus*; *Guara alba*; *Plegadis falcinellus*; *Platalea leucorodia*, *alba*, *regia*, *flavipes*, *ajaja*.

FAMILY PHOENICOPTERIDAE, Flamingos. 2/4, fig. 10.

Species examined: *Phoenicopterus ruber*; *Phoeniconaias minor*.

The starch gel patterns of the Ardeidae are uniform. The conalbumins characteristically migrate cathodally, those of *Ixobrychus* more so than those of the typical herons. Component 18 migrates less than 1.0 cm anodally from the application point, but the ovomucoid migrates well toward the anode, thus creating a rather large area in the pattern lacking major protein components. Some small bands occur in this region in a number of patterns, but in others only a broad, indistinct streak is evident. The variation of these components seems to be of little significance.

Close to the well-defined ovomucoid and anodal to it is the ovalbumin, which, in patterns from fresh material, separates into three bands; the middle one is usually the most concentrated. In older material they merge into a single, broad band. These bands, even in fresh samples, are not as distinct as those in the patterns of the Phalarocoridae and Phasianidae. A prealbumin migrates anodal to the ovalbumin.

The pattern of *Cochlearius* is similar in all respects to that of the Ardeidae. The patterns of the Ciconiidae and the Threskiornithidae differ slightly from those of the Ardeidae and from each other. Both patterns have an ovalbumin of slightly lower mobility than that of the Ardeidae. In some samples a small amount of subdivision of the ovalbumin is observable, but it is not as conspicuous as in the patterns of the herons. The usual appearance is of a dense ovalbumin band with a smaller, less concentrated band anodal to it (see patterns of *Mycteria americana* and *Threskiornis spinicollis*, fig. 9). There is also the possibility that this band is a prealbumin since these species lack the prealbumin well anodal to the ovalbumin, which is present in the heron patterns.

The patterns of the Threskiornithidae agree with those of the Ardeidae in having cathodally migrating conalbumins. They differ from those of the Ardeidae in having an ovomucoid of lower mobility. The patterns of the Ciconiidae differ from those of both the Ardeidae and Threskiornithidae in that their conalbumins migrate anodally between the origin and Component 18. The ovomucoid of the ciconiids moves slightly less toward the anode than that of the threskiornithids. In all aspects the pattern of *Scopus umbretta* agrees best with those of the Ciconiidae.

Resemblances between the patterns of the Ardeidae and those of the Anatidae are found in the number and arrangement of the ovalbumins. However, the ovalbumin region of the herons has a greater anodal mobility than that of the ducks, and in other aspects of the pattern the two groups are different. The patterns of the Ardeidae and Threskiornithidae are similar to those of the Accipitridae and Cathartidae in possessing cathodally migrating conalbumins, but the falconiform families have a single ovalbumin, which migrates more slowly than that of the herons. The patterns of the herons show more similarities to those of the diurnal birds of prey than do those of the storks. The ovalbumin patterns of ibises and storks resemble those of the Sulidae in shape and mobility. The stork patterns also agree with those of the sulids in the position of the conalbumins, but the ovomucoids differ in mobility.

We conclude that the egg white pattern of *Cochlearius* is most like that of the Ardeidae. The patterns of the Threskiornithidae show more resemblances to those of the Ardeidae than do the patterns of the Ciconiidae, but the patterns of all three groups are basically alike. The pattern of *Scopus* is most like those of the Ciconiidae.

The egg white patterns of the flamingos *Phoenicopterus ruber* and *Phoeniconaias minor* are identical. The ovalbumin is like that of storks in mobility and in lacking subdivision into three components. The ovomucoid has a mobility like that of many

ciconiiform birds. The conalbumins migrate between the origin and Component 18, thus agreeing with the patterns of the storks. The egg white patterns of the flamingos are unlike those of the Anatidae in these respects, but they agree with the pattern of the screamer *Chauna torquata* in the mobility and shape of the ovalbumin.

Comparisons to the patterns of other groups reveal no striking similarities. Thus the egg white patterns of the flamingos are more similar to those of the Ciconiiformes, especially the Ciconiidae, than they are to those of the Anseriformes or any other group.

CONCLUSIONS

The ciconiiform birds considered here seem to form a natural assemblage, but the degrees of relationship among the groups and within each group remain to be defined more precisely. The differences between the herons and storks, for example, in both their anatomy and their electrophoretic patterns, seem best explained in terms of divergence from a common ancestor during a long evolutionary history.

On the basis of the egg white data and all previous studies *Cochlearius* seems best placed within the Ardeidae. The hypothesis that *Cochlearius* is closely allied to the night herons (*Nycticorax*) is reasonable, but it has not been proved.

Both *Scopus* and *Balaeniceps* are certainly ciconiiforms. The egg white evidence suggests that *Scopus* may be allied to the storks, but this problem needs additional study. Since egg white of *Balaeniceps* has not yet been available for study, we decline to offer an opinion concerning its closest allies within the order.

We agree with Sibley, Corbin, and Haavie (1969) that the flamingos are ciconiiform. The morphological, immunological, and biochemical data suggest that the Ciconiiformes and Anseriformes are more closely related to each other than either one is to any other group of birds. Obviously, more data are needed to clarify the degree of relationship, but the inclusion of these two orders in a superorder seems justified. We find little or no evidence in the egg white patterns to suggest a close relationship between the Ciconiiformes and either the Pelecaniformes or the Falconiformes. The degrees of relationship to other orders remain to be defined more precisely.

ORDER ANSERIFORMES

Suborder Anhimae

Family Anhimidae, Screamers

Suborder Anseres

Family Anatidae, Ducks, Geese, Swans

Wetmore, 1960

INTRODUCTION

The principal systematic problems concerning the waterfowl are: (1) the relationships between the Anseriformes and other orders; (2) the relationship between the screamers (Anhimidae) and the typical waterfowl (Anatidae); (3) the relationships among the genera of ducks, geese and swans.

As will become apparent in the following review of the literature, the flamingos, the gallinaceous birds and the herons have been mentioned most frequently as possible relatives of the Anseriformes.

That the members of the Anatidae constitute a closely knit group is attested by several lines of evidence, including the frequency of hybridization among seemingly diverse species (Sibley, 1957; A. Gray, 1958; Johnsgard, 1960d). The Anhimidae, although differing in many ways from the Anatidae, also share with them a number of seemingly important characters. They are placed within the Anseriformes because there is not better evidence linking them to some other order. Beddard (1898a) has reviewed this problem.

HISTORICAL REVIEW OF THE CLASSIFICATION

Pre-Darwinian classifications of the waterfowl were reviewed by Fürbringer (1888) and Gadow (1893). Although most of this older literature has little bearing on the questions posed above, it is instructive that Nitzsch (1840) found that the pterylosis

of the typical waterfowl is uniform among the members of the group, suggesting close relationships, but also distinctive when compared with that of other orders. He placed the Anatidae between the Procellariiformes and Pelecaniformes in a large assemblage of aquatic birds. The Anhimidae differ from the Anatidae in having the feathering continuous, i.e., they lack apteria.

The first important study producing evidence of a relationship between the screamers and the waterfowl was that of Parker (1863). He noted that the skull of *Chauna chavaria* differs in no important way from that of the ducks and that the sternum of the screamers is "thoroughly anserine." Parker considered the pelvis of the anatine genus *Plectropterus* to be "exactly intermediate" between that of a goose and that of a screamer.

Huxley (1867) placed the waterfowl and screamers in the Chenomorphae, which he considered to be related to the flamingos and ciconiiform birds. He thought that the screamers may be distantly allied to the Cracidae. These opinions were based primarily on skull characters.

Garrod (1873d, 1874a) thought that the screamers were related to the gallinaceous birds and the rails, and that the Anatidae were close to the penguins, the loons, and the grebes. In a later study of the pterylosis, visceral anatomy, osteology, and myology of screamers Garrod (1876b) pointed out resemblances to the ratites and the Ciconiiformes.

In their review of many New World species of waterfowl P. Sclater and Salvin (1876) recognized a single family (Anatidae) composed of seven subfamilies.

The trachea of *Biziura* is simple in structure like that of the *Erismatuinae* (= *Oxyurini*) (Forbes, 1882d).

The screamers have a horizontal fibrous septum passing across the abdominal cavity and covering the intestine (Beddard, 1886b). A similar structure is found in the storks. In the same paper Beddard described the subcutaneous air cells of the screamers, which he believed to be modified pre- and post-bronchial air sacs. He also pointed out that the bronchial air sacs of storks and flamingos are divided by septa into several chambers.

Fürbringer (1888) placed the waterfowl in his Pelargornithes, which included the ciconiiform birds, diurnal raptors and grebes. He divided the Anatidae into the subfamilies Anserinae, Cygninae, Anatinae, and Merginae, and assigned the screamers to a separate but adjacent suborder.

Shufeldt (1888a) reported on the osteology of several North American waterfowl. Beddard and Mitchell (1894) and Mitchell (1895) described the anatomy of the three species of Anhimidae.

Sharpe (1891) and Gadow (1893) admitted the Anseres and Palamedeae (= Anhimae) as suborders in their Anseriformes. Salvadori (1895) divided the 205 species in his Anatidae into 11 subfamilies and 64 genera. His Chenomorphae included suborders for the screamers and flamingos.

From osteological characters Seebohm (1889) concluded that the Anseres, composed of the Cygnidae and Anatidae, were related both to the flamingos and to the Ciconiiformes. In Seebohm's opinion, the screamers represent a connecting link between the Anseres and the Galliformes.

Three families were established in the Anseres by Seebohm (1895): Anatidae, Palamedeidae [= Anhimidae], and Phoenicopteridae.

Shufeldt's (1901b) comparison of the skeletons of *Anhima*, *Coscoroba* and *Meleagris* revealed that the screamer resembled the goose or the turkey in most characters. However, he believed that it was not closely allied to either, and agreed with Fürbringer (1888) that the screamers constitute a separate group. Shufeldt concluded (p. 461) that the screamers should be "placed near the Anseres" but "between

the latter and the ostrich type of birds.”

From a study of skeletal characters Pycraft (1906) recommended that the Erismaturinae (= *Oxyura*, *Thalassornis*, *Biziura*) should be merged with the Fuligulinae (= Aythyinae) while such genera as *Histrionicus*, *Melanitta*, *Tachyeres* and *Somateria* should be placed together in the Somateriinae.

In 1911 Heinroth published an important paper on the behavior of waterfowl in which he presented the idea that behavior patterns are clues to relationships. His work has influenced subsequent comparative behavioral studies on waterfowl, especially those of Lorenz (e.g., 1941).

The microscopic structure of waterfowl feathers suggested “high specialization” to Chandler (1916). He felt that such genera as *Branta*, *Anser*, and *Cygnus* link the Anseriformes to the flamingos. The feather structure of the screamers is peculiar in many respects, and Chandler was unable to associate them with any other group of birds.

E. Stresemann’s (1927–34) classification followed Fürbringer’s (1888), and that of Peters (1931) resembled Salvadori’s (1895). For 167 species Peters used 62 genera, 42 of which were monotypic. Generic splitting was carried to an extreme by von Boetticher (1941, 1942); he recognized 84 genera, 55 of them monotypic.

A. Miller (1937) studied the adaptations in skeletal and muscular anatomy of *Nesochen* (= *Branta*) *sandvicensis* to life on the dry lava uplands of Hawaii. He concluded that this species was closely related to *Branta* and pointed out that *Chloephaga* differed considerably from the anserines. On the basis of 115 characters he separated *Chen*, *Anser*, *Philacte*, *Nesochen* and *Branta*.

DeMay (1940) gave details on the subcutaneous air cells of the screamer *Chauna chavaria*. She showed that the cervical air sacs are continuous with the air cells, which cover the main part of the body as well as the extremities. The bones are pneumatic, even to the digits. In pelicans, boobies, gannets and tropic birds, which dive into the water from considerable heights, the subcutaneous air cells cushion the impact, but their function in the screamers is unknown.

Parallel but independent investigations led to joint papers by Delacour and Mayr (1945, 1946) proposing a classification based on tarsal pattern, tracheal structure, plumage patterns of downy young adults, hybridization and behavior. This work developed from earlier studies by Delacour (1936, 1938) but gained importance because it was one of the first to recognize that widespread hybridization among waterfowl indicated close relationships. Delacour and Mayr also argued against the recognition of monotypic genera based on the secondary sexual characters of males. The conclusions of these authors were similar to Heinroth’s, but they treated more species. Because their work has formed a basis for subsequent studies, their arrangement is given below.

Family Anatidae

Subfamily Anserinae

Tribe Anserini: *Branta*, *Anser*, *Cygnus*, *Coscoroba*

Tribe Dendrocygnini: *Dendrocygna*

Subfamily Anatinae

Tribe Tadornini: *Lophonetta*, *Tadorna*, *Alopochen*, *Nesochen*, *Cyanochen*, *Chloephaga*, *Cereopsis*, *Tachyeres*

Tribe Anatini: *Anas*, *Hymenolaimus*, *Malacorhynchus*, *Rhodonessa*, *Stictonetta*

Tribe Aythyini: *Netta*, *Aythya*

Tribe Cairinini: *Amazonetta*, *Chenonetta*, *Aix*, *Nettapus*, *Sarkidiornis*, *Cairina*, *Plectropterus*, *Anseranas*

Tribe Mergini: *Somateria*, *Melanitta*, *Histrionicus*, *Clangula*, *Bucephala*,
Mergus

Tribe Merganettini: *Merganetta*

Tribe Oxyurini: *Oxyura*, *Biziura*, *Thalassornis*, *Heteronetta*.

According to Glenny (1944b; 1955: 561), all Anseriformes are bicarotid (A-1 pattern), and there are no significant differences between Anhimidae and Anatidae in the carotid arrangement.

On the basis of quadrate morphology Friant (1947) concluded that the Anhimae are the survivors of an ancient group which was ancestral to both flamingos and waterfowl.

Von Boetticher and Eichler (1951) presented a classification based upon the distribution of certain genera of Mallophaga of the family Acidoproctidae. *Anseranas* is uniquely parasitized by *Heteroproctus* and was placed in a monotypic family, Anseranatidae. The Anserae and Cygnae are distinguished by being the hosts of the genus *Ornithobius*. The mallophagan genus *Acidoproctus* is found on the Tadorneae, Dendrocygnae, Hymenolaimeae, Aythyae and Cairineae, and no acidoproctids parasitize the Mergeae, Somatereae and Anateae.

Additional suggestions concerning waterfowl relationships were made by Timmerman (1963) based upon a study of the *Ornithobius* complex of the mallophagan family Philopteridae. He found *Ornithobius* to be parasitic on geese and swans, *Bothriometopus* on screamers, and *Acidoproctus* on *Anseranas*, *Dendrocygna*, *Alopochen*, *Plectropterus*, *Netta*, and *Aythya*. Two groups of swans were recognized by Timmermann, one consisting of *Cygnus olor*, *melanocoryphus*, and *atratus*, the other of *Cygnus cygnus*, *buccinator*, and *columbianus*. He thought that *Dendrocygna arborea* is more closely related to *D. autumnalis* than to *D. guttata*. *Dendrocygna guttata* and *eytoni* seem to be closely allied to *D. arcuata* and *javanica*, but *D. bicolor* and *viduata* form a rather distinct pair of species.

Mayr and Amadon (1951) included the Anhimidae and Anatidae in their order Anseres and agreed with von Boetticher (1943) that *Anseranas* deserves to be placed in a tribe of its own.

The morphology of the chromosomes of about 50 species of waterfowl were studied by Yamashina (1952). He concluded that all Anseriformes are similar, and his classification recognized a limited number of genera. However, he separated the wood duck (*Aix sponsa*) from the mandarin duck (*Dendronessa* [= *Aix*] *galericulata*) because of the apparently aberrant karyotype of the mandarin. The wood duck has a normal anatine karyotype and has hybridized with a large number of other anatine species but hybrids involving the mandarin duck have been considered rare or non-existent (A. Gray, 1958). It has been suggested by some authors that the chromosomal differences may function as a reproductive isolating mechanism. Johnsgard (1968) reported some apparently valid hybrids between the mandarin and two other species, namely, the wood duck and the Laysan mallard (*Anas platyrhynchos laysanensis*). These hybrids are probably infertile. Thus, although the mandarin has now been shown to be capable of hybridization with other anatines it is obviously not as able to hybridize as is the wood duck and many other anatines. Whether or not the aberrant karyotype is the basis for this condition remains, as it was, an intriguing but unproved hypothesis.

Delacour (1954) followed the classification that he and Mayr (1945) had proposed, except for two major changes: *Anseranas* was placed in a separate subfamily, and the tribe Merganettini was merged with the Anatini.

Verheyen (1953; 1955a,b) reopened the investigation of waterfowl osteology. From his extensive measurements of bones he concluded that the Anseriformes are

polyphyletic and divided them into 16 families, seven of which are monotypic. Verheyen (1956g) gave the screamers ordinal status, and judged that they are most closely related to *Anseranas* and distantly allied to the Casuariidae. In 1961 he reduced most of his "families" to subfamily or tribal status, but dismissed the significance of numerous waterfowl hybrids by arguing that "evidence was accumulating that the inbreeding situation, in a group of more or less related species, is general and, [like] any other organic feature, susceptible to vary in its numerous attributes from group to group" (p. 19). Verheyen's opinion on the significance of hybridization cannot be taken seriously. The significance of hybridization in general and in the Anatidae in particular was discussed by Sibley (1957, 1961) and by Johnsgard (1960d).

Serological evidence led Cotter (1957) to conclude that *Aix* and *Cairina* are more closely related to each other than either is to *Anas*, thus supporting the allocation of *Aix* and *Cairina* to the tribe Cairinini.

Humphrey (1958) studied the trachea and the tracheal bulla in *Melanitta*, *Clangula*, *Bucephala*, *Mergus* and the eiders. He suggested that the eiders are closest to the Anatini and should be placed next to them in the Somateriini. He also proposed the merger of *Lampronetta* with *Somateria*.

The paper electrophoretic patterns of the egg white proteins of 56 species of Anatidae were examined by Sibley (1960). He concluded that "the Anatidae are a very closely related group" although *Anseranas* and *Dendrocygna* each has a distinctive egg white pattern.

Both Wetmore (1951a, 1960) and Storer (1960a) divided the Anseriformes into the suborders Anhimae (screamers) and Anseres (typical waterfowl).

From evidence on cranial morphology and kinesis, Simonetta (1963) postulated a common origin for the waterfowl and gallinaceous birds.

As a result of extensive studies on waterfowl behavior Johnsgard contributed a number of opinions on relationships within the Anatidae (1960a-f; 1962; 1963; 1964; 1965a,b; 1966a,b; 1967). Those differing from the classification of Delacour and Mayr (1945) are:

- 1) *Anseranas* placed in a separate family.
- 2) *Cereopsis* moved from Tadornini to Anserini.
- 3) *Stictonetta* seems to have anserine affinities.
- 4) *Tacheyeres* placed in a separate tribe.
- 5) *Callonetta* moved from Anatini to Cairinini.
- 6) *Merganetta* moved from Anatini to Aythyini.
- 7) *Rhodonessa* moved from Anatini to Aythyini.
- 8) *Thalassornis* moved from Oxyurini to Dendrocygnini.

Woolfenden (1961) compared the postcranial osteology of most genera of waterfowl. He favored subordinal rank for the screamers and, within the Anatidae, recognized the subfamilies Anatinae and Anserinae. He proposed the following changes in the classification of Delacour and Mayr:

- 1) *Anseranas* placed in a separate family.
- 2) *Stictonetta* moved from Anatini to Dendrocygnini.
- 3) *Cereopsis* placed in a monotypic tribe.
- 4) *Plectropterus* moved from Cairinini to Tadornini.
- 5) *Tacheyeres* moved from Tadornini to Anatini.
- 6) Tribe Cairinini merged with Anatini.
- 7) *Merganetta* placed in a separate tribe.
- 8) *Rhodonessa* moved from Anatini to Aythyini.

The peculiarities of *Anseranas* are adaptations to living in tropical swamps, according to behavioral and ecological studies by Davies and Frith (Davies, 1961,

1962a,b; 1963; Davies and Frith, 1964; Frith and Davies, 1961). They found the behavior of *Anseranas* to be like that of the Anserini.

Frith (1964a,b) concluded that the freckled duck (*Stictonetta naevosa*) is not anatine, but may be closest to the swans of the tribe Anserini. His decision was based on behavior, plumage of downy young, and tracheal anatomy.

The earliest fossil definitely belonging to the Anseriformes is *Eonessa*, described by Wetmore (1938) on the basis of wing bones from the middle Eocene of Utah. Apparently this was a small duck about the size of modern *Oxyura*. An earlier form is *Gallornis*, described by Lambrecht (1931) from Cretaceous deposits in France. Although Lambrecht (1933) and others thought that *Gallornis* was an early anseriform, Brodkorb (pers. comm.) believes that it may be ancestral to the flamingos.

Howard (1964a), in her review of the fossil Anseriformes, noted that by Oligocene time the Anserinae and Anatidae are represented in the fossil record. Many modern genera and several modern tribes were apparently present in the Miocene. To Howard about ten Pliocene species are indistinguishable from present-day species. Some distributional changes have occurred. For example, members of the tribe Tadornini apparently inhabited North America during the Pleistocene (Howard, 1964a,b).

By comparing the structure and composition of the egg shells of the Anatidae, Tyler (1964) obtained data of possible taxonomic value. In a plot of total shell nitrogen against shell thickness, *Anseranas* was well separated from other species. There was a linear sequence involving *Cygnus*, *Coscoroba*, *Anser*, and *Branta*. The Dendrocygnini lay "in a separate area of the graph from the Anserini . . . and some distance from *Anseranas*," while the Tadornini were "almost but not quite separate from the Dendrocygnini, but clearly separate from the Anserini" (p. 534). *Plectropterus* fell near *Anser*, the Oxyurini near the Dendrocygnini, and *Chauna* near *Branta*. When insoluble shell nitrogen was plotted against total shell nitrogen, most tribes were close together, but *Dendrocygna* was partially separated, with *Anseranas* and *Cereopsis* even more distant. *Chauna* fell between *Dendrocygna* and *Cereopsis*.

Baker and Hanson (1966) compared the hemoglobins and serum proteins of eight species of *Anser* and three of *Branta* using starch gel electrophoresis. They found only minor variations, which further indicates the close relationships among the geese.

The study by Ploeger (1968) presents interesting data on the effects of the last Pleistocene glaciation on the geographic variation of arctic Anatidae but it is not pertinent to the questions posed in the present paper.

SUMMARY

From the available evidence it seems clear that the members of the Anatidae, regardless of the categorical subdivisions preferred by different authors, constitute a monophyletic group of approximately 147 living species. Anatomically they tend to be remarkably uniform and the frequency of hybridization, even across tribal and subfamilial lines, argues eloquently for this conclusion. Even *Anseranas*, which is usually considered the most aberrant genus, is thought to be anserine by those who have studied it in greatest detail in the field (Davies and Frith, cited above).

The evidence for the relationships of the Anhimidae seems to indicate that they are most closely related to the Anatidae but there are just enough differences between the two groups to keep the question open. Are the skull and other characters proof of common ancestry or could they be due to convergence? The absence of a reasonable

alternative to an alliance with the Anatidae is lacking and the long-accepted arrangement should not be disturbed. Neither should it be completely accepted without further proof.

The nearest relatives of the Anseriformes are probably the flamingos, the ciconiiforms and perhaps the galliforms but all are distant, at best, and the degrees of relationship are unknown.

THE EGG WHITE PROTEIN EVIDENCE

ORDER ANSERIFORMES

FAMILY ANHIMIDAE, Screamers. 1/3, fig. 10.

Species examined: *Chauna torquata*.

FAMILY ANATIDAE, Ducks, Geese, Swans. 89/147, figs. 10-12.

Species examined (nomenclature follows Johnsgard, 1965b): *Anseranas semipalmata*; *Dendrocygna bicolor*, *javanica*, *arborea*, *autumnalis*; *Cygnus olor*, *atratus*, *melanocoryphus*, *columbianus*; *Anser cygnoides*, *fabalis*, *albifrons*, *anser*, *indicus*, *caerulescens*, *rossi*, *canagicus*; *Branta sandvicensis*, *canadensis*, *leucopsis*, *bernicla*, *ruficollis*; *Cereopsis novaehollandiae*; *Chloephaga melanoptera*, *picta*, *poliocephala*, *rubidiceps*; *Neochen jubatus*; *Alopochen aegyptiacus*; *Tadorna tadorna*; *Tachyeres patachonicus*; *Plectropterus gambensis*; *Cairina moschata*, *scutulata*; *Sarkidiornis melanotos*; *Pteronetta hartlaubi*; *Nettion coromandelianus*; *Callonetta leucophrys*; *Aix sponsa*, *galericulata*; *Chenonetta jubata*; *Amazonetta brasiliensis*; *Hymenolaimus malacorhynchus*; *Merganetta armata*; *Anas penelope*, *americana*, *sibilatrix*, *strepera*, *crecca*, *capensis*, *gibberifrons*, *platyrhynchos*, *rubripes*, *undulata*, *poecilorhyncha*, *luzonica*, *specularioides*, *acuta*, *georgica*, *erythrorhyncha*, *versicolor*, *punctata*, *querquedula*, *discors*, *cyanoptera*, *smithi*, *clypeata*; *Aythya ferina*, *americana*, *fuligula*, *affinis*, *australis*, *marila*; *Malacorhynchus membranaceus*; *Marmaronetta angustirostris*; *Somateria mollissima*, *spectabilis*; *Clangula hyemalis*; *Melanitta nigra*; *Bucephala albeola*, *islandica*; *Mergus cucullatus*, *albellus*, *serrator*; *Oxyura jamaicensis*, *maccoa*, *vittata*, *australis*; *Biziura lobata*.

The starch gel patterns of the Anatidae are fairly uniform. On the cathodal side of the application point in many patterns a crescent-shaped band of lysozyme is seen. It is likely that all species have lysozyme and its apparent absence in some patterns is probably due to a lower concentration of protein being applied to the gel. The first band anodal to the application point is Component 18. It appears to be double in many, if not all, patterns of waterfowl and is seen best in the patterns of *Anas punctata* and *A. platyrhynchos*. The conalbumins migrate anodal to Component 18 in a dense cluster of two or three bands. The position of the conalbumins varies even within a genus and in some ducks it occurs midway between the application point and the ovalbumin. Thus, in the waterfowl, the Galliformes and the Columbiformes the conalbumins migrate the farthest anodally of the non-passerine groups.

Between Component 18 and the conalbumins occur some other small fractions. Usually they are seen as a poorly defined smear, but in the patterns of *Dendrocygna* two fairly sharp bands are seen. The identity of these proteins is not known. Anodal to the conalbumins is the ovomucoid region, which varies in concentration and in the number of constituent bands. The definition of these bands often is poor, but in some patterns (e.g., *Dendrocygna*) three may be seen. The heterogeneity of the

ovomucoids is thought to be due to differences in the composition of the carbohydrate moiety rather than to differences in the amino acid sequence (Feeney, Osuga, and Maeda, 1967). In dilute patterns from fresh material the ovalbumin region resolves into two or three bands. Three bands can be seen in the pattern of *Anas punctata*. The arrangement and shape of these bands is unlike that of the Galliformes and Pelecaniformes, two other groups in which the ovalbumin is multiple.

There are no consistent differences in pattern between members of the sub-families Anserinae and Anatinae, nor are there consistent similarities among members of the tribes proposed by Delacour and Mayr (1945). The starch gel pattern of *Anseranas* is similar to those of many other species of waterfowl. Perhaps the most distinct anserine group is represented by patterns of members of the genus *Dendrocygna*. They have a distinctively large number of well-defined bands in the various regions of the pattern, but a more significant difference is the slower-moving ovalbumin. Also, in patterns of *Dendrocygna* the middle ovalbumin component is the most concentrated, whereas in the patterns of other ducks the most anodal band is the most concentrated.

The pattern of the screamer *Chauna torquata* differs from those of the Anatidae and seems to be "intermediate" between those of ducks and those of some ciconiiforms. The ovalbumin apparently has two components and migrates more slowly than those of ducks. This aspect of the pattern is identical to that of the spoonbill *Platalea alba*. The pattern of *Chauna* has a faint ovomucoid, which is unlike the ovomucoids of either ducks or herons. The conalbumins are clustered together as in the ducks, but they migrate less toward the anode than those of ducks. The conalbumins of ciconiiform birds are more widely separated from one another (i.e., are not closely clustered together) and those of the Ardeidae and Threskiornithidae migrate cathodally. Component 18 of *Chauna* migrates less toward the anode than it does in the anseriform and ciconiiform patterns. Thus the pattern of *Chauna* shows similarities to those of both the Anseriformes and Ciconiiformes. It does not resemble closely the patterns of other orders.

The patterns of the waterfowl are similar to those of some of the ciconiiform birds in the position of Component 18 and in the number and mobility of the ovalbumins. Some herons share the heterogeneity of the ovomucoid with the ducks. The patterns of the waterfowl resemble those of the gallinaceous birds in having a multiple ovalbumin and similar mobilities of the conalbumins, but there are many differences in detail between the patterns of these two groups. The patterns of the waterfowl are unlike those of other palmate, or totipalmate, swimming birds.

CONCLUSIONS

The members of the Anatidae form a closely related group of species, but the results of this study cannot be used to suggest relationships within the family.

On the basis of previous studies, the egg white patterns and the evidence from the tryptic patterns of ovalbumin and hemoglobin, the Anseriformes appear to be allied to the flamingos and to the ciconiiform birds more closely than to any other group. The egg white patterns of the Anhimidae suggest no relationships except to a duck-flamingo-heron assemblage but they are so peculiar in a number of characters that further study of their relationships is required before a final decision can be made.

ORDER FALCONIFORMES

Suborder Cathartae

Superfamily Cathartoidea

Family Cathartidae, New World Vultures

Suborder Falcones

Superfamily Sagittarioidea

Family Sagittariidae, Secretarybirds

Superfamily Falconoidea

Family Accipitridae, Hawks, Old World Vultures, Harriers

Family Pandionidae, Ospreys

Family Falconidae, Falcons, Caracaras

Wetmore, 1960

INTRODUCTION

The diurnal raptors evolved early in the history of birds and today are represented by several well-differentiated groups. These groups share many characters but they also exhibit marked differences, thus raising the possibility that convergence may account for at least some of the similarities. The major groups, and the problems relating to their taxonomic relationships, are as follows:

1) Cathartidae. The New World vultures differ in many characters from the other falconiforms and they are usually separated as a suborder. It is possible that the cathartids are similar to the other falconiforms only through convergence but the presently available evidence can be interpreted either for or against this hypothesis. Thus at least two questions remain to be answered: (a) are the New World vultures most closely related to the diurnal raptors or, if not, (b) which are their closest living relatives?

2) *Sagittarius*. The secretarybird of Africa seems to be a cursorial falconiform but it is aberrant in many ways and resembles, superficially at least, the cariamas (Cariamidae: Gruiformes) of South America. Although the evidence seems to indicate that *Sagittarius* is falconiform the remaining doubt needs to be dispelled.

3) Falconidae. The genus *Falco* is usually placed with the caracaras (Polyborinae), *Herpetotheres*, *Micrastur* and the falconets (*Microhierax*, *Polihierax*,

Spizapteryx) in a suborder within the Falconiformes. However, a considerable array of evidence has been interpreted as suggesting that the falcons may actually be more closely related to the owls than to the typical hawks and this possibility remains unresolved.

4) *Pandion*. The relationships of the osprey within the Falconiformes have frequently been debated. The closest relatives are still in doubt and its proper taxonomic rank is uncertain.

5) *Accipitridae*. The "typical" diurnal birds of prey, including the kites, honey buzzards, hawks, eagles, harriers and Old World vultures, apparently constitute an unquestionably monophyletic assemblage. Their possible relationships to the Cathartidae, *Sagittarius*, the falcons and *Pandion* require clarification and their closest living relatives among other orders remain uncertain.

HISTORICAL REVIEW OF THE CLASSIFICATION

Nitzsch (1840) designated the raptorial birds as one of his eight main avian assemblages. The "Raubvögel", or Accipitrinae, contained the diurnal raptors, Old World vultures, New World vultures, and owls. Nitzsch found that the four groups could be distinguished from one another on the basis of pterylography. G. Gray (1844-1849) likewise placed the birds of prey in a single group at the beginning of his linear sequence.

The Aetomorphae of Huxley (1867) included all raptorial birds, although he conceded that they varied widely in many characters. The four "groups" that he recognized were Strigidae (owls), Cathartidae (New World vultures), Gypaetidae (hawks, eagles, falcons and Old World vultures) and Gypogeranidae (secretarybird). In his list the birds of prey occur between the Pelecaniformes and Psittaciformes.

Sharpe (1874) divided his Accipitres into two suborders, the Falcones and Pandiones. Within the Falcones he recognized the family Vulturidae for both New and Old World vultures, and the Falconidae for the falcons. He included *Sagittarius* and *Cariama*, as well as the South American caracaras, in the subfamily Polyborinae of his Falconidae.

The Falconidae, Cathartidae, and Sagittariidae were "impossible to unite in any intimate way", according to Garrod (1873d, 1874a). He thought the Cathartidae belong between the Pelargi (storks) and Herodiones (herons). In his classification the Accipitres follow the Steganopodes (Pelecaniformes) and include the families Falconidae and Strigidae, and both the Cathartidae and Accipitres are cohorts within his order Ciconiiformes. He placed *Sagittarius* along with *Cariama* and the bustards in the Otidae, a family in his Galliformes.

Ridgway (1875) divided the Falconidae into two subfamilies with subgroups, roughly equivalent to tribes, as follows: Falconinae (Falcones, Polybori, Micrastures, Herpetotheres, Pandiones), Buteoninae (Pernes, Buteones).

P. Sclater (1880) placed his Striges and Accipitres in adjacent orders and within the latter recognized the families Falconidae, Cathartidae, and Serpentariidae. Reichenow's (1882) order Raptatores included the families Vulturidae (Old and New World vultures), Falconidae, and Strigidae. Barrows (1885) offered a similar arrangement for his order Accipitres, accepting the families Gypogeranidae (*Sagittarius*), Cathartidae, Falconidae (including the Old World vultures and *Pandion*), and Strigidae.

Several basic patterns in the arrangement of the secondary coverts were apparent to Goodchild (1886, 1891). One of these, which he termed the accipitrine style, was common to the Psittaciformes, Strigiformes, Accipitres (excluding *Pernis*, *Pandion*, and *Sagittarius*), Anseriformes, Ardeidae, and Phalacrocoracidae. Goodchild found that the arrangement of these feathers in the Cathartidae is most like that of *Leptoptilos*, *Pelecanus*, *Fregata*, *Sula*, *Anhinga*, and the Procellariidae.

Fürbringer (1888) acknowledged the families Gypogeranidae (*Sagittarius*), Cathartidae, and Gypo-Falconidae within his gens Accipitres. He placed the Accipitres between the ciconiiform and pelecaniform birds in his suborder Ciconiiformes.

A separate order for the Cathartidae was erected by Sharpe (1891). His order Accipitriformes contained the other raptorial birds in the four suborders Serpentarii, Accipitres, Pandiones, and Striges. He considered *Pandion* to be intermediate between the hawks and owls and recognized the families Vulturidae and Falconidae within his Accipitres.

Gadow agreed with Fürbringer that the Falconiformes are allied to the Ciconiiformes and Pelecaniformes. Within the order he (1893) separated the suborders Cathartae and Accipitres and divided the latter into four families: Gypogeranidae, Vulturidae, Falconidae, and Pandionidae.

Shufeldt published a study of the osteology of the Cathartidae (1883b) and described the osteology of *Circus cyaneus* (1889a). Later (1891b) he found osteological peculiarities among American kites which prompted him to separate this group as the family Elanidae with the genera *Elanus*, *Elanoides*, and *Ictinia* each in separate subfamilies. In his 1904b classification Shufeldt divided his supersuborder Accipitriformes into two superfamilies. The Falconoidea contained the Serpentariidae, Falconidae, Milvidae, Pandionidae, and Vulturidae. The Cathartidae were the sole members of his other superfamily, the Cathartoidea. In a detailed paper on the osteology of North American raptors Shufeldt (1909) did not alter his earlier classification, but discussed the relationships of the Falconiformes to other groups. He felt that alliances to some or all of the Pelecaniformes, Ciconiiformes, Psittaciformes, and *Cariama* (Gruiformes) were possible and suggested that further comparative studies be made. In 1919 Shufeldt described the osteology of the Philippine monkey-eating eagle (*Pithecophaga jefferyi*), concluding that it is most closely related to the harpy eagle (*Harpia harpyja*) of South America. Finally, Shufeldt (1922) wrote on the osteology of the wedge-tailed eagle (*Aquila audax*) of Australia.

A subclass Falconiformes containing the orders Raptores and Psittaci was established by Seebohm (1890a). The suborders Serpentarii (*Sagittarius*), Accipitres, and Striges made up the Raptores. On the basis of the deep plantar tendons Seebohm (1890c) placed the Cathartidae in his subclass Coraciiformes, which also contained members of Wetmore's (1960) Coraciiformes, Caprimulgiformes, Coliiformes, and Apodiformes. Seebohm noted that in this group the hallux is always present and receives its tendon from the flexor perforans digitorum, not from the flexor hallucis longus. This is another example of the nonsense that can emerge from blind dependence upon a single character. Seebohm (1895) expressed less certainty in his placement of the Cathartidae but maintained them as a separate order in his subclass Falconiformes, recognizing the orders Psittaci, Accipitres, and Striges. *Sagittarius* was placed in a monotypic family in his Accipitres.

Beddard (1889b, 1898a) was aware of the variation among the falconiforms, although he admitted both *Sagittarius* and the Cathartidae into his Accipitres. He pointed out that the Cathartidae differed in the condition of eight characters (after-shaft, oil gland, muscle formula, accessory semimembranosus, caeca, syrinx, basioccipital processes, and type of desmognathism) and questioned their inclusion within

the Falconiformes. Beddard commented on similarities between the Cathartidae and Ciconiiformes and felt that the Pelecaniformes are "not far off."

The osteology of the diurnal birds of prey was studied by Sushkin (1899a,b; 1900a,b; 1905). His interest was mainly in the suborder Accipitres, in which he recognized the families Aquilidae and Falconidae (including *Falco*, *Polihierax*, *Herpetotheres*, and the South American caracaras). Although he excluded *Sagittarius* and *Pandion* from the Accipitres, Sushkin found many points of similarity between the Accipitres and the kites such as *Pernis*, *Aviceda*, *Elanoides*, and *Leptodon*.

The osteology of the Falconiformes was also investigated by Pycraft (1902). He divided the order into three suborders: Serpentarii, Cathartae, and Accipitres (with families Falconidae and Buteonidae). He believed that the Cathartidae are the most primitive members of the order and that the entire group shares more characters in common with the Gruiformes than with the Ciconiiformes. Pycraft also commented: "On osteological grounds . . . it is doubtful whether the Striges would ever have been separated from the Accipitres" (p. 314), but on the basis of soft part anatomy he thought that the owls belong among the "picarian" birds.

In the patterns of intestinal coiling Mitchell (1901a) discerned few similarities between the Cathartidae and the Ciconiiformes, and he found nothing to suggest an alliance between *Sagittarius* and *Cariama*. Although Mitchell did not mention any comparisons between hawks and owls, Beddard (1910) observed that the Falconiformes and Strigiformes share several characteristics of the alimentary tract not found in other birds.

Reichenow (1913-14) was convinced of a hawk-owl relationship and ranked each group as a suborder within his order Raptatores. To Chandler (1916), however, there was little in the structure of their feathers to support such an alliance. The Cathartidae show an "astonishing likeness" to *Anhinga* in the nature of the distal barbules of the inner vane. The feather structure of *Sagittarius* is more like that of the Accipitridae than that of the Cathartidae. Chandler concluded that the Falconiformes were most likely derived from pelecaniform ancestors.

In 1924 Swann began publishing a monograph on the birds of prey. After Swann's death in 1926 Wetmore assumed responsibility for the remaining portions, the last of which was published in 1945. In his order Accipitres Swann recognized the families Cathartidae, Aegypiidae, Sagittariidae, and Falconidae. He placed *Pandion* in a subfamily next to the falcons.

The order Accipitres of E. Stresemann (1927-34) contained the families Cathartidae, Sagittariidae, and Falconidae. He put *Pandion* among the Aquilinae of his Falconidae.

Wetmore (1940, 1951, 1960) divided his order Falconiformes into the suborders Cathartae and Falcones. Within the Falcones, he proposed the superfamilies Sagittarioidea and Falconoidea, the latter containing the Accipitridae, Pandionidae, and Falconidae. Peters (1931) followed the same arrangement except that he included *Pandion* in the Accipitridae.

There are three types of pterylosis in the Falconiformes—the accipitrid type, the falconid type, and the cathartid type (Compton, 1938). In both pterylosis and arrangement of the plantar tendons *Pandion* resembles the cathartids, and Compton concluded that it was best placed in a separate family within the suborder Cathartae. He also thought that *Sagittarius* is more closely related to the Accipitridae than to the other falconiforms.

The pterylosis of the California condor (*Gymnogyps californianus*) was described by A. Miller and Fisher (1938). Fisher (1939, 1942, 1943, 1944, 1946, 1947) published additional studies on the pterylosis, osteology, and myology of the Cathart-

idae. His 1946 study of locomotor adaptations in these birds was one of the first thorough analyses of the functional anatomy of an avian group. Although he did not make critical comparisons to other birds of prey, he felt that *Cathartes* and *Coragyps* are more closely allied to each other than either is to another group composed of *Sarcorhamphus*, *Gymnogyps*, and *Vultur*. The complete pelvic muscle formulae for the cathartids as reported by Fisher (1946) is ACDXY Am V for *Cathartes* and *Coragyps* and CDXY Am V for *Sarcorhamphus*, *Gymnogyps* and *Vultur*.

Hudson (1948) compared the pelvic musculature of two New World vultures (*Cathartes*, *Coragyps*), the secretary-bird (*Sagittarius*), the osprey (*Pandion*), four genera of Accipitridae (*Accipiter*, *Buteo*, *Aquila*, *Circus*), and three falcons (*Falco*). He confirmed the pelvic muscle formula found for the cathartids by Fisher (1946) and noted that it differs considerably from that of *Sagittarius* (BDXY Am V) and the other falconiform birds (AD Am). He also discovered many other points in which the Cathartidae and *Sagittarius* differ from each other and from other Falconiformes. "It appears quite possible that the American vultures, secretary bird and the hawk and falcon tribe represent three entirely different lines of avian evolution and are no more closely related to each other than to the owls. . . . If these three lines were derived from a common source subsequent adaptive radiation has greatly obscured the original similarity of muscle pattern in the pelvic limb. I strongly suspect that the 'hawkish' appearance of *Sagittarius* has been developed through convergent evolution" (p. 127). Hudson considered *Pandion* to be a "somewhat aberrant offshoot" of the hawk-falcon group and placed it in a separate suborder of the Falconiformes.

Berlioz (1950) put the Falconiformes and Strigiformes next to each other, thus implying the possibility of a distant relationship. Howard (1950) reviewed the fossil record and found that the cathartid vultures, secretarybirds, and typical hawks were distinguishable by Eocene time. She pointed out that a cathartid vulture (*Plesio-cathartes*) occurred in the Eocene of France. Although a number of fossil falconiforms are known, they seem to shed little light on the relationships among the groups. Mayr and Amadon (1951), citing unpublished observations by Wetmore, were skeptical about the allocation of *Plesiocathartes* and they were equivocal regarding the place of the Cathartidae and *Sagittarius*. These authors reported (p. 6) a "verbal communication" from McDowell suggesting that the Cathartidae may be "representatives of some ancient American radiation which may even include . . . the Anhimidae, Cracidae, and Tinamidae." This interesting speculation is apparently not supported by evidence.

The evidence from the Mallophaga suggests that the Falconiformes are monophyletic (Clay, 1950, 1951, 1957). The distinctive and specialized genus *Falcolipeurus* is found only on *Sagittarius*, *Cathartes*, *Coragyps*, *Vultur*, and larger members of the Accipitridae. Found on the same Falconiformes, but also on some other avian groups, is the genus *Laembothrion*. *Cuculiphilus* parasitizes *Gyps*, *Pseudogyps*, and the Cathartidae, but is also found on the Cuculidae. Another genus (*Kurodia*) is found elsewhere only on the Strigiformes. Von Boetticher and Eichler (1954) supported Clay's opinion with additional work on the Mallophaga. They felt that all groups except the Cathartidae and *Sagittarius* could be included in the Falconidae.

Barnikol (1951, 1953, 1954), Starck and Barnikol (1954), and Starck (1959) presented evidence from a study of the jaw musculature innervated by the trigeminus nerve that the falcons are more similar to the owls than to other diurnal birds of prey. For example, *Falco tinnunculus* and *Strix aluco* show almost identical muscle proportions in spite of differences in external appearance and various quantitative characters of the skull, brain, and eyes. These authors formed their conclusions

cautiously and were careful not to ascribe too much importance to their findings. Jollie (1953) agreed with Barnikol and Starck and placed the falcons in a separate order next to a combined caprimulgid-form-strigiform group. In Jollie's opinion, the New World vultures are best considered as a suborder within a procellariiform-pelecaniform assemblage, and *Sagittarius* is most closely related to *Cariama*. Voipio (1955) accepted the evidence of these workers and declared the Falconiformes to be polyphyletic.

An interesting example of the concordance of several characters leading to a determination of relationships is provided by *Gampsonyx swainsonii*, a South American raptor. This species, which resembles a small falcon in proportions, had been placed in the Falconidae near *Polihierax* and *Spizapteryx* by Peters (1931: 281) and Hellmayr and Conover (1949: 288). Plótnick (1956) examined characters of the bill, nostrils, and scutellation of the tarsus and toes and concluded that *Gampsonyx* is not a falcon but is related to the kites (*Elanus*).

Clay (1958) discovered that *Gampsonyx*, unlike any falcon, is parasitized by a species of *Degeeriella* (Mallophaga) of the same species-group as that found on *Elanus*. V. Stresemann (1959) found that *Gampsonyx* molts its primaries in the "descending" manner from the first to the tenth as do the members of the Accipitridae. She agreed that its nearest relatives are *Elanus*, *Elanoides*, and the other kites. Finally, Brodkorb (1960) pointed out that *Gampsonyx* is like the Accipitridae, not the Falconidae, in all of its skeletal features. He thus corroborated the earlier opinions of Sushkin (1905) and Friedmann (1950) who, on the basis of osteology, placed *Gampsonyx* near the kites.

Differences in the molt patterns among the Falconiformes have been clarified by Mebs (1960), Piechocki (1955; 1956; 1963a,b), Sutter (1956), V. Stresemann (1958), V. and E. Stresemann (1960), and E. and V. Stresemann (1966). In falcons the primary molt begins with primary no. 4 and proceeds in both directions. The secondaries are renewed from two foci. The outer focus is usually at secondary no. 5 from which the molt wave proceeds in both directions. Another region of molt begins with the innermost secondary and proceeds in descending fashion. In falcons the tail molt is centrifugal (i.e., from the inner to the outer rectrices) except that the outermost (sixth) rectrix is usually lost before R1 or R2. In *Falco peregrinus* the sequence is R1-2-6-3-4-5. The tail molt in *Falco vespertinus* apparently is irregular.

In the Accipitridae the molt of the primaries begins with primary no. 1 and moves in descending fashion to no. 10. This plan has been found in *Gypohierax*, *Circus*, *Geranospiza*, several genera of Accipitrinae (including *Accipiter*, *Kaupifalco*, and *Butastur*), in the Milvinae, Perninae, and Elaninae. There are usually three foci for the molt of the secondaries in the Accipitridae. In *Circus macrourus*, for example, molt proceeds in the ascending manner from secondaries 1, 5 and 8 or 9. The Stresemanns (1966: 334) reported that the tail molt of the Accipitridae is irregular with a tendency toward a transilient mode (for example: rectrices 1-6-4-2-3-5 or 6-1-4-5-3-2).

Verheyen (1957c) excluded *Sagittarius* from the Falconiformes and placed it and the Cariamidae in an order Cariamiformes. He adhered to this position in his classification (1959b) of the remaining falconiform birds, but later (1961) replaced *Sagittarius* in the Falconiformes. Verheyen concluded that the diurnal birds of prey are allied on one hand with the Cuculiformes and on the other with a columbid-psittacid group. His 1961b classification follows:

Suborder Sagittarii: Sagittariidae
 Suborder Cathartes: Cathartidae

Suborder Falcones: Polyboridae, Falconidae

Suborder Pandiones: Pandionidae

Suborder Accipitres: Buteonidae, Aegypiidae, Elanidae, Pernidae.

The egg white protein patterns of *Cathartes* and *Coragyps* are more similar to accipitrids such as *Buteo* and *Buteogallus* than to the Old World vultures *Torgos* and *Gyps* (Sibley, 1960). The patterns of *Torgos* and *Gyps* are similar to those of *Elanus* and *Ictinia*; thus the Accipitridae, although variable, appeared to share a common pattern type. The patterns of the Falconidae were unlike those of the Accipitridae. "There are just enough similarities between *Athene* and *Caracara*, for example, to make one cautious; but there are so many differences that the egg-white patterns cannot be used as evidence in favour of a falcon-owl relationship" (p. 242).

May (1962) described the dermocranium and chondrocranium of the embryo tawny owl (*Strix aluco*). Comparisons with the embryo of the kestrel (*Falco tinnunculus*) revealed a number of similarities, but other species were not examined.

Peakall (1963) hydrolyzed purified ovalbumins from several species of birds and separated the constituent amino acids by ascending paper chromatography. The plots of optical density against distance for three different samples of the crow *Corvus brachyrhynchos* were virtually identical. As expected, different groups had dissimilar patterns. Three species of Accipitridae (*Accipiter gentilis*, *Buteo jamaicensis*, and *Aquila chrysaetos*) were compared with the cathartid (New World) vultures *Coragyps atratus* and *Cathartes aura*. The data supported the conclusion that the Cathartidae are not closely related to other Falconiformes.

Voous and Wijsman (1964) suggested that the genera *Cassinaetus* and *Stephanoetus* should be merged with *Spizaetus*.

Histological studies of the egg shells (Tyler, 1966) have revealed few major differences among the Falconiformes, except that the shells of some species have vacuoles or spaces in the outer layers. The shell vacuoles are present in *Accipiter*, *Buteo*, *Aquila*, *Pernis*, *Milvus*, *Haliaeetus*, *Gyps*, *Sarcogyps*, and *Pandion*. They are lacking in the Cathartidae, Falconidae, and *Sagittarius*, and possibly lacking in *Gypaetus barbatus* and *Neophron percnopterus*. All of the shells with vacuoles show an unetched outer layer when examined in plastic-embedded radial sections, and thin sections show spaces between and within the crystals. The Falconidae differ from the Accipitridae in the ratio between total nitrogen and soluble nitrogen of the shell, but *Pernis* and *Pandion* are intermediate. Tyler pointed out, however, that *Pandion* differs from the Accipitridae only in this feature.

Ligon (1967) reexamined various characters of the cathartid vultures and concluded that they are allied to the storks and not to the other diurnal raptors. He proposed an order Ciconiiformes, apart from the Ardeiformes, to contain these groups as two suborders. The characters he cited in favor of such a relationship included several from osteology, the condition of the patagial tendons, thigh muscle formulae, nestling plumage, and poor development of the syrinx.

In their important monograph on the Falconiformes, L. Brown and Amadon (1968) did not suggest any obvious ties between the birds of prey and other orders, but they did not dismiss the possibility of a distant relationship to the owls. "For what they are worth, the falcons (or at least the typical falcons of the genus *Falco*) differ from Accipitridae and agree with Strigidae, owls, in the following ways: absence of nest-building instinct (in all but caracaras); killing of prey by biting and severing neck vertebrae, holding of food in one claw, hissing by young to show fear or threat and some movements of curiosity, e.g., head bobbing" (p. 24).

Brown and Amadon suggested many possible relationships within the order. To

discuss them would require considerable space but their linear classification to the generic level indicates most of the proposed relationships. (Genera in parentheses are thought to be most closely allied.)

Suborder Cathartae

Family Cathartidae

Cathartes, *Coragyps*, *Sarcorhamphus*, *Gymnogyps*, *Vultur*; (relationships to others unclear).

Suborder Accipitres

Family Pandionidae

Pandion; (possible distant affinity to kites).

Family Accipitridae

Kites: (*Aviceda*, *Leptodon*, *Chondrohierax*, *Henicopternis*, *Pernis*, *Elanoides*, *Machaerhamphus*); (*Gampsonyx*, *Elanus*, *Chelictinia*); (*Rosthramus*, *Harpagus*, *Ictinia*, *Lophoictinia*, *Hamirostra*, *Milvus*, *Haliastur*).

Fish eagles: *Haliaeetus*, *Ichthyophaga*; (possible alliance to kites).

Old World vultures: *Gypohierax*, *Neophron*, *Gypaetus*, *Necrosyrtes*, *Gyps*, *Torgos*, *Sarcogyps*, *Aegyptius*, *Trigonoceps*; (possible alliance to fish eagles).

Snake eagles: *Circaetus*, *Terathopius*, *Spilornis*, *Dryotriorchis*, *Eutriorchis*; (may have evolved from kites).

Harrier hawks, crane hawks, harriers: *Polyboroides*, *Geranospiza*, *Circus*; (linked to snake eagle group through *Polyboroides*).

Sparrow hawks and goshawks: *Melierax*, *Megatriorchis*, *Erythrotriorchis*, *Accipiter*, *Urotriorchis*; (thought to be allied to the harriers, through *Melierax*, and to *Buteo*).

Sub-buteonines: *Butastur*, *Kaupifalco*, *Leucopternis*, *Buteogallus*, *Harpyhaliaeetus*, *Heterospizias*, *Busarellus*, *Geranoaetus*, *Parabuteo*.

Buteos: *Buteo*.

Harpy eagles: *Morphnus*, *Harpia*, *Harpyopsis*, *Pithecophaga*.

Booted eagles: *Ictinaetus*, *Aquila*, *Hieraetus*, *Spizastur*, *Lophoetus*, *Spizaetus*, *Stephanoetus*, *Oroaetus*, *Polemaetus*.

Family Sagittariidae

Sagittarius; (possibly related to the eagles).

Suborder Falcones

Family Falconidae

Aberrant Neotropical genera: (*Milvago*, *Phalcoboenus*, *Polyborus*, *Daptrius*); *Herpetotheres*; *Micrastur*; (may be allied to typical falcons through *Milvago*).

Falconets and falcons: *Spizapteryx*, *Polihierax*, *Microhierax*, *Falco*.

Vuilleumier (1970) recognized only two genera for the caracaras: *Daptrius* for the forest species and *Polyborus* (to include *Phalcobaenus* and *Milvago*) for the non-forest species.

SUMMARY

The Falconiformes as constituted here have been thought to be related to the Strigiformes, Ciconiiformes, Pelecaniformes, and Gruiformes. The proposed alliance to the owls was originally based on external characters and the similarities have long been

considered to be due to convergence, but data from the trigeminal musculature reopened the possibility of a falcon-owl relationship. Evidence also has been accumulating from studies of osteology, wing molts, and biochemical characters which suggests that the falcons may not be closely allied to the other diurnal birds of prey. Some of the data also seem to link the falcons with the owls but there is no proof of such an alliance.

The Cathartidae are aberrant in many ways and some authors have stressed the differences in osteology and soft-part anatomy and used them in support of a cathartid-ciconiid or cathartid-pelecaniform alliance. Relationship to a coraciiform assemblage also has been postulated.

Most authors have concluded that *Sagittarius* is falconiform, but they have failed to present convincing evidence on its nearest relatives within the order. Some have considered *Sagittarius* to be allied with *Cariama* but the obvious possibilities of convergence between these two genera cast doubt on the proposal.

Pandion has always been thought to be falconiform. Most of the controversy about *Pandion* has concerned its taxonomic rank. Many authorities have regarded it as allied to the larger hawks and eagles, some to the Cathartidae, and others to the owls.

Although the diurnal birds of prey are all similarly adapted, they are variable in most respects. Many single characters, or an appropriate combination of several, could be used to argue for polyphylety. The Mallophaga can be used to support a belief in the monophylety of the Falconiformes but the possibilities of convergence cast doubt on the validity of all data on the distribution of parasites.

Thus, the long-standing uncertainties concerning the relationships of the diurnal birds of prey remain unresolved but the problems are clearly defined.

THE EGG WHITE PROTEIN EVIDENCE

ORDER FALCONIFORMES (nomenclature follows L. Brown and Amadon, 1968)

FAMILY CATHARTIDAE, New World Vultures. 2/7, fig. 12.

Species examined: *Cathartes aura*; *Coragyps atratus*.

FAMILY PANDIONIDAE, Osprey. 1/1, fig. 13.

Species examined: *Pandion haliaetus*.

FAMILY ACCIPITRIDAE, Hawks, Eagles, Old World Vultures. 62/217, figs. 13-15.

Species examined: *Pernis apivorus*; *Machaerhampus alcinus*; *Elanus leucurus*, *caeruleus*, *notatus*; *Ictinia plumbea*, *mississippiensis*; *Lophoictinia isura*; *Milvus migrans*; *Haliaastur sphenurus*; *Haliaeetus leucogaster*, *vocifer*, *albicilla*; *Gypohierax angolensis*; *Neophron percnopterus*; *Gyps africanus*, *rueppellii*, *coprotheres*; *Torgos tracheliotus*, *Trigonoceps occipitalis*; *Circaetus gallicus*; *Terathopus ecaudatus*; *Spilornis cheela*; *Polyboroides typus*; *Circus assimilis*, *aeruginosus*, *cyaneus*, *pygargus*; *Melierax metabates*, *canorus*; *Accipiter gentilis*, *melanoleucus*, *nisus*, *tachiro*, *fasciatus*, *soloensis*, *badius*, *cooperii*; *Kaupifalco monogrammicus*; *Buteogallus anthracinus*; *Heterospizias meridionalis*; *Parabuteo unicinctus*; *Buteo magnirostris*, *lineatus*, *platypterus*, *swainsoni*, *albi-caudatus*, *polyosoma*, *jamaicensis*, *buteo*, *lagopus*, *rufofuscus*; *Aquila rapax*, *wahlbergi*, *chrysaetos*, *audax*; *Hieraaetus fasciatus*, *pennatus*, *morphnoides*; *Lophaetus occipitalis*; *Spizaetus cirrhatus*; *Polemaetus bellicosus*.

FAMILY SAGITTARIIDAE, Secretarybird. 1/1, fig. 15.

Species examined: *Sagittarius serpentarius*.

FAMILY FALCONIDAE, Falcons, Caracaras. 17/61, fig. 15.

Species examined: *Polyborus plancus*; *Milvago chimango*; *Polihierax semitorquatus*; *Falco naumanni*, *rupicoloides*, *sparverius*, *tinnunculus*, *cenchroides*, *columbarius*, *berigora*, *subbuteo*, *longipennis*, *eleanorae*, *concolor*, *biarmicus*, *cherrug*, *peregrinus*.

The egg white protein patterns of the Falconiformes in starch gel vary; so we will consider the groups separately.

A simple pattern is shared by most members of the Accipitridae including *Accipiter*, *Buteo*, *Aquila*, *Circus*, *Spilornis*, and *Hieraaetus*. In fresh, undenatured specimens, the conalbumins, usually three, migrate cathodally but in older samples they move anodally as a smear. Component 18 migrates about 1.0 cm anodally. A single ovomucoid, not sharply defined, migrates about 4.0 cm anodally from the origin. The ovalbumin, also single, migrates about 1.0 cm cathodal to the buffer front. At the buffer front a prealbumin usually is present.

The patterns of *Elanus* and *Circus* differ from that described above only in having an additional band in the ovalbumin region. This appears as a small crescent-shaped band anodal to the main ovalbumin component.

The pattern of *Pandion* agrees with those of the Accipitridae in all respects, its ovalbumin matching those of *Elanus* and *Circus* most closely.

The patterns of the Old World vultures are uniform and differ from those of "typical" accipitrids by having two or three ovalbumin components with a lower mobility than the single ovalbumin of the accipitrids. The most cathodal component is a small, sharp band, and it is separated from the larger and more concentrated middle component. The middle and the most anodal bands are not well separated, and together they produce a broad region in the pattern which appears to have a constriction in its middle.

The pattern of *Sagittarius* is like those of the Accipitridae with a single ovalbumin. It differs from those in having conalbumins that migrate anodal to Component 18. This conalbumin difference may be unimportant. Another problem is that simple patterns, like that of *Sagittarius*, with a single ovalbumin and ovomucoid and with anodally migrating conalbumins, occur in a number of non-passerine groups, thus raising the question of electrophoretic coincidence. Finally, a critical comparison of *Sagittarius* and *Cariama* cannot be made because the available patterns of the latter are from poor material and therefore untrustworthy.

The patterns of the cathartid vultures do not resemble closely those of the storks or of any other group although their cathodally migrating conalbumins are shared with the Accipitridae and also with the herons. Because a few other non-passerines also have cathodal conalbumins these similarities must be considered unimportant. The available patterns of *Cathartes* and *Coragyps* differ in minor ways from one another but these differences must be unimportant because hybrids between these genera have been reported (A. Gray, 1958).

The cathartid patterns do not support the suggested alliances to the Pelecaniformes or Procellariiformes (Jollie, 1953) or to the Anhimidae, Cracidae or Tinamidae (Mayr and Amadon, 1951).

The patterns of the Falconidae differ from those of the other Falconiformes in most respects. The conalbumins migrate anodal to Component 18 and the ovomucoid separates into two distinct bands, the more cathodal of which is larger and more concentrated. The ovalbumin region, which migrates faster than that of the accipitrids, consists of three well-defined components. A small weak band is preceded anodally by a dense, broad component. The most anodal band is small and crescent-shaped. The sharpest patterns in the synoptic plates are those of *Falco tinnunculus* and *F. sparverius*. The pattern of *Milvago chimango* is like that of *Falco* except that the conalbumins migrate cathodally as in the accipitrids and cathartids.

The patterns of the falcons are unlike those of the hawks and match almost exactly those of the owls, especially *Tyto*. The multiple ovalbumins of some accipitrids like *Elanus*, *Circus*, and the Aegypiinae differ from those of *Falco* in arrangement, shape, and mobility. There is less overall resemblance between accipitrids and *Falco* patterns than between *Falco*, *Tyto* and the strigid owls.

CONCLUSIONS

The questions concerning the relationships of the Falconiformes are some of the most challenging in avian systematics. The problems are complicated by the uncertain affinities of several falconiform groups and conflicting evidence from a variety of sources.

The egg white evidence suggests that the Cathartidae are allied to the Accipitridae but does not prove it. A study of their affinities should be undertaken, and such a study should include comparisons to the Ciconiiformes (particularly the storks), the Pelecaniformes and various other groups.

We believe that *Pandion* is related to the Accipitridae and that most of its peculiarities can be explained as adaptive responses to its way of life.

Sagittarius, although somewhat aberrant, is probably related to the Accipitridae but until fresh egg white from the Cariamidae can be examined we will defer judgment.

The true falcons differ from the diurnal birds of prey in a number of respects and show some similarities to the owls. Whether the falcons thus form a link between the falconiforms and strigiforms or merely are convergent to the hawks is not known. This intriguing problem is worthy of intensive investigation.

ORDER GALLIFORMES

Suborder Galli

Superfamily Cracoidea

Family Megapodiidae, Megapodes

Family Cracidae, Curassows, Guans, Chachalacas

Superfamily Phasianoidea

Family Tetraonidae, Grouse

Family Phasianidae, Quails, Pheasants, Peacocks

Family Numididae, Guineafowl

Family Meleagrididae, Turkeys

Suborder Opisthocomi [see below under Cuculiformes]

Family Opisthocomidae, Hoatzins

Wetmore, 1960

INTRODUCTION

The usual two questions—relationships within the order and to other orders—apply to the Galliformes as they do to other groups. The high frequency of hybridization, even between seemingly diverse genera, argues for a closely knit core of species but there are some satellite groups, such as the megapodes, which present special problems.

The hoatzin (*Opisthocomus*) has often been thought to be galliform and was placed in the suborder Opisthocomi of the Galliformes by Wetmore (1960). Egg white protein and other evidence indicates to us that *Opisthocomus* is a cuckoo, allied to the crotophagine genera *Guira* and *Crotophaga*, and its affinities are discussed under the Cuculiformes.

The relationships of the gallinaceous birds to other orders poses some fascinating problems which remain to be solved. Are the tinamous related more closely to the ratites, to the galliforms or to some third group? Are the anseriforms related to the galliforms via the screamers? Several other groups have also been proposed as possible relatives, as the following review will indicate.

HISTORICAL REVIEW OF THE CLASSIFICATION

Lilljeborg (1866) placed the Phasianidae and Tetraonidae, along with the Crypturidae (= Tinamidae) and Pteroclididae (sandgrouse) in his order Gallinae. He separated the Megapodiidae and Penelopidae (= Cracidae) and put them in the order Pullastrae, which included the columbiform birds.

Huxley's order Alectoromorphae encompassed the Turnicidae, Phasianidae, Pteroclididae, Megapodiidae, and Cracidae. "The Turnicidae approach the Charadriomorphae, the Pteroclididae the Peristomorphae [= Columbidae]; while the Cracidae have relations with the birds of prey on one hand, and with *Palamedea* [= *Anhima*] and the other Chenomorphae on the other" (1867: 459). Huxley (1868b) proposed, on the basis of foot structure, the "suborders" Peristopodes, containing the Cracidae and Megapodiidae, and the Alectoropodes, including the Phasianidae, Meleagrididae, and Numididae.

P. Sclater and Salvin (1870) followed Huxley in subdividing the Cracidae into the Penelopinae and Cracinae on the basis of characters in the "postacetabular area." In addition, they recognized a separate subfamily for *Oreophasis derbianus*.

In his Galliformes Garrod (1873d, 1874a) listed such groups as the Struthionines and Psittaci. His cohort (β) Gallinaceae was composed of the Palamedeidae, Gallinae, Rallidae, Otidae, Musophagidae, and Cuculidae. Later Garrod (1879) extended J. Müller's (1847) work on syringeal structure. He studied the tracheae of numerous galliform birds, but discovered little about their relationships. He thought that the genera *Argusianus*, *Lophortyx*, and *Coturnix* belong in the Coturnicinae, and that *Phasianus*, *Lagopus*, *Perdix*, and possibly *Meleagris* form part of the Phasianinae. He considered *Numida* and *Gallus* difficult to place and, for reasons not entirely clear, maintained the Cracidae as a separate family.

P. Sclater (1880) separated his Gallinae into the Peristeropodes (= Cracidae, Megapodiidae) and Alectoropodes (= Phasianidae, Tetraonidae). Elliott (1885) followed the same arrangement. Reichenow (1882) included the Megapodiidae, Cracidae, Opisthocomidae, Phasianidae, Perdidae, and Tetraonidae in his order Rasores. He divided the Phasianidae into the subfamilies for the peafowl and typical pheasants and recognized New World and Old World groups within the Perdidae.

The morphology of gallinaceous birds in general was studied by Parker (1864, 1891b) and that of the Cracidae by Gadow (1879). Shufeldt described the osteology of North American grouse (1881b), *Gallus bankiva* (1888c), and the turkeys (1914a).

The Gallinae of Seebohm (1888b) consisted of the suborders Crypturi, Gallinae, Pterocletes, and Columbidae. The Phasianidae, Cracidae, and Megapodiidae made up a suborder Gallinae, which he considered intermediate between the tinamous and sandgrouse. Seebohm (1890a) expanded this group to include the loons, grebes, rails, and shorebirds, and renamed it the order Gallo-Grallae. In 1895 Seebohm revised his previous opinions: his earlier suborder Gallinae was renamed Galli and with it in the Galliformes was the suborder Psophiae for the Cariamidae, Psophiidae, Opisthocomidae, and Podidae (= Heliornithidae). The other families that he once considered close to the Galliformes were placed among the Charadriiformes, Gruiformes, and Turniciformes.

Sharpe (1891) required five families to express his concept of relationships within the Phasiani: Phasianidae, Tetraonidae, Perdidae, Numididae and Meleagrididae. The Galliformes of Gadow (1892) contained as suborders the Turnices (including *Pedionomus*) and the Galli, which he divided into the families Gallidae

and Opisthocomidae. He (1893) recognized the families Megapodiidae and Cracidae within his Galli. In both classifications Gadow placed the Galliformes next to the Tinamiformes and Gruiformes. Fürbringer (1888, 1902) felt that the Galliformes was comprised only of the Megapodiidae, Cracidae, and Gallidae. Ogilvie-Grant (1893) followed essentially the same arrangement as P. Sclater (1880) and Elliott (1885).

Many similarities in the arrangement of the secondary coverts between gallinaceous birds and tinamous were found by Goodchild (1886, 1891). He emphasized that the "wing style of the tinamous differs in no essential respect . . . from that of the Gallinae" or Hemipodii (1891: 324). H. Clark (1898) found that the New World quails differ from grouse in their pterylography. He (1901b) placed the fowls and tinamous in his "galliform birds." Dwight (1900) described but did not comment on the molts of the North American Tetraonidae in which he included the New World quails.

Beddard (1898a) reviewed the works of his predecessors and concluded that "the Galli seem to be . . . an ancient group of birds" with relationships to the tinamous and the Anseriformes.

In a study of feather structure Chandler (1916) found the Galliformes similar to one another. The megapodes and cracids, in his opinion, show affinities to the Cuculiformes, while the Phasianidae seem to be allied to the Columbidae. Chandler also concluded that "unmistakable relationship is also shown to the Tinami, which, according to feather structure, should be considered as a specialized offshoot from a primitive gallinaceous stem" (p. 342). Chandler included the Turnicidae and *Pedionomus* in a separate suborder in his Galliformes.

W. D. Miller (1924) reviewed the condition of the fifth secondary in birds and noted that the Galliformes are eutaxic except for some genera of megapodes. *Leipoa* and *Alectura* are eutaxic but *Megapodius* and *Megacephalon* are diastataxic.

Following Fürbringer, E. Stresemann (1927-34) recognized three families of galliform birds. His Phasianidae was divided into the Numidinae, Meleagridinae, and Phasianinae. Peters (1934) separated the Cracidae and Megapodiidae within a superfamily Cracoidea, and within the Phasianoidea he retained family status for the Tetraonidae, Phasianidae, Numididae, and Meleagrididae.

Hachisuka (1938) classified the gallinaceous birds mainly on the color and shape of feathers, egg color, and geographical distribution. He recognized the families Megapodidae, Cracidae, Tetraonidae, and Phasianidae and within the Phasianidae admitted four subfamilies and 58 genera, nearly half of which were monotypic.

Lowe (1938) investigated the anatomy of *Afropavo congensis*, but found that "the Phasianidae are osteologically so uniform in structure that it is difficult to find characters to distinguish the various groups" (p. 226). He tentatively concluded that *Afropavo* is an "unspecialized generalized or primitive peacock," closest to the Pavoninae and Argusianinae.

Mayr and Amadon (1951) reduced the guinea fowls and grouse to subfamily rank within the Phasianidae, but Wetmore (1951, 1960) preferred to maintain these groups as separate families. Storer (1960a) followed Wetmore's classification. In his monograph of the pheasants Delacour (1951a) divided the 49 species into 16 genera.

The gallinaceous birds are osteologically homogeneous in Verheyen's (1956d) view. He recognized the families Megapodiidae, Cracidae, and Phasianidae, with a number of subfamilies and tribes in each. His (1961) Galliformes included as suborders the Tinami, Opisthocomi, and Turnices.

A. Gray (1958), as well as Peterle (1951) and Cockrum (1952), listed many instances of hybridization between galliform birds. Sibley (1957) pointed out that the numerous "intergeneric" and "interfamilial" hybrids are proof of close relationships

and that this emphasizes the taxonomic weakness of monotypic genera based solely on the secondary sexual characters of males.

Although hybrids have occurred among the New World quail genera *Colinus*, *Lophortyx*, *Callipepla*, and *Oreortyx* (Bailey, 1928; Compton, 1932; McCabe, 1954; Banks and Walker, 1964; Johnsgard, 1970, 1971), hybridization with other phasianids is not substantiated. Seth-Smith (1906) mentioned a hybrid *Lophortyx californicus* × *Ammoperdix heyi* but gave no details. From a study of molt and pterylography Ohmart (1967) suggested that *Callipepla* and *Lophortyx* be merged. Johnsgard (1970: 87) recommended that *Lophortyx* and *Callipepla* be merged with *Colinus*.

Sibley (1960) found that the egg white protein patterns of the galliform birds were similar in paper electrophoresis and felt that only the Megapodiidae and Phasianidae deserved family status. The other groups that Peters (1934) recognized as families were reduced to subfamily rank within the Phasianidae. *Opisthocomus* was not available for study.

Immunological data were used as indices to relationships within the Galliformes by Mainardi (1958, 1959, 1960, 1963) and Mainardi and Taibel (1962). These findings suggested that *Phasianus*, *Meleagris*, and *Numida* are closely related and that even subfamily status for each is not warranted. Although he retained the Cracidae and Megapodiidae, Mainardi considered it unnecessary to recognize the superfamily Cracoidea for them. *Numida* was considered to be closest to the cracids. *Coturnix* and *Gallus*, although generally similar to the phasianids, were widely separated from each other and from other genera.

The appendicular musculature of gallinaceous birds was examined by Hudson and his colleagues (Hudson, Lanzillotti, and Edwards, 1959; Hudson and Lanzillotti, 1964; Hudson et al., 1966). They measured the lengths of muscles and widths of muscle bellies, and compared them with the aid of a computer. The hoatzin (*Opisthocomus*) differed from all the galliforms studied (see account below under Cuculiformes). The principal proposals on galliform classification by Hudson and his co-workers are as follows:

- 1) To place the Megapodiidae and Cracidae in a superfamily Cracoidea.
- 2) To separate the grouse as a family (Tetraonidae) on the basis of quantitative data, the absence of the adductor digiti II muscle, the presence of a sesamoid in the extensor indicis longus, and the feathering of the tarsus.
- 3) Within the Phasianidae to recognize the subfamilies Numidinae, Meleagridinae, Pavoninae, Odontophorinae, and Phasianinae.

The embryological evidence suggests that megapodes are specialized and probably evolved from a pheasant-like ancestor (G. Clark, 1960; 1964a,b). Differences in feather structure at hatching indicated to Clark that megapodes and cracids are not closely related.

Holman (1961) compared the osteology of living and fossil New World quails. He concluded that they represent a separate family, and, on the basis of pelvic structure, he recognized two groups.

Data from agar electrophoresis of the soluble proteins of the eye lens and of skeletal, heart, and stomach muscle of several Galliformes, convinced Gysels and Rabaey (1962) that *Afropavo congensis* should be treated as a monotypic subfamily, remotely allied to *Pavo*. Hulsemans (1962) reached a similar conclusion from a study of the hind limb musculature of *Afropavo*.

Simonetta (1963) hypothesized a common origin for the Anseriformes and Galliformes. His opinion was based on a detailed study of the skull.

Data on the fossil Galliformes were summarized by Brodkorb (1964). The Megapodiidae are represented only in the upper Pleistocene; the earliest form assigned to the Cracidae is *Palaeophasianus meleagroides* Shufeldt (1913) from lower Eocene

deposits of Wyoming. The Odontophorinae are known from the lower Oligocene, the Phasianinae from the upper Oligocene, the Tetraoninae from the lower Miocene, and the Meleagridinae from the upper Pliocene. There are no known extinct species of Numidinae.

Vuilleumier (1965) demonstrated that the casques, wattles, and areas of naked skin in cracids are merely species-specific recognition marks. He reduced the number of genera in the Cracidae to seven, lumping *Pipile* in *Penelope*, and *Nothocrax*, *Mitu* and *Pauxi* into *Crax*. *Chamaepetes* and *Aburria* are "very close" to *Penelope*. *Penelopina* is intermediate between *Ortalis* and *Penelope*, while *Oreophasis* is "somewhat aberrant." Vuilleumier thought that the Cracidae probably originated in the warmer parts of Tertiary North America and radiated there before reaching South America. He also postulated that North American ancestors of *Ortalis*, *Penelope*, and *Crax* colonized South America during the Pleistocene.

In a series of notes culminating in a monograph of the Cracidae, Vaurie (1964, 1965a-c, 1966a,b; 1967a-d, 1968) disputed the conclusions of Vuilleumier and restored those genera which that author had lumped. Vaurie considered *Penelopina* "aberrant in virtually all characters," and did not agree with Vuilleumier that it is intermediate between *Ortalis* and *Penelope*. *Ortalis* and *Penelope* are "very closely related, as no line can be drawn between them that is not breached by one character or another" (1968: 166). Vaurie recognized three tribes within the Cracidae, with their constituent genera as follows: Penelopini (*Ortalis*, *Penelope*, *Pipile*, *Aburria*, *Chamaepetes*, *Penelopina*); Oreophasini (*Oreophasis*); Cracini (*Nothocrax*, *Mitu*, *Pauxi*, *Crax*).

E. and V. Stresemann (1966) and E. Stresemann (1965, 1967) found a distinctive molt pattern in the Cracidae, and among phasianids a centrifugal tail molt distinguishing the Perdicinae.

The evidence on grouse, especially that on egg color and plumages of downy young was reviewed by Short (1967). From these data as well as a reevaluation of morphological characters and evidence from hybridization, he reduced the number of genera of grouse from the eleven of Peters (1934) to six. The Tetraoninae "evolved along with turkeys (Meleagridinae) and New World quail (Odontophorinae) from early North American phasianid stock" (p. 34).

Arnheim and Wilson (1967) examined the lysozymes of the species of Galliformes by micro-complement fixation. An antiserum against chicken (*Gallus*) lysozyme was used as the reference, and the lysozymes of other species were tested for their reactivity to it. The partridges (*Alectoris*, *Francolinus*) and the New World quails reacted strongly to the anti-*Gallus* antiserum, but the pheasants, usually thought to be the closest relatives of *Gallus*, reacted relatively weakly. To check this unexpected result Arnheim, Prager, and Wilson (1969) compared the amino acid compositions and tryptic peptide maps of the lysozymes of the bob-white quail (*Colinus virginianus*) and the ring-necked pheasant (*Phasianus colchicus*) with that of the chicken. Their results indicated that the lysozymes of *Colinus* and *Gallus* are most alike, differing only by two amino acid substitutions. The lysozymes of *Gallus* and *Phasianus* possibly differed in as many as seven residues. Antisera were prepared against the lysozymes of *Colinus* and *Phasianus*, and micro-complement fixation tests confirmed the earlier findings, namely, that *Colinus* and *Gallus* are virtually identical and that *Phasianus* could be distinguished from both.

The amino acid sequences of the lysozymes of the chicken (*Gallus*) (Canfield, 1963a,b; Canfield and Anfinsen, 1963), turkey (*Meleagris gallopavo*) (LaRue and Speck, 1970) and the Old World quail (*C. coturnix*) (Kaneda, et al., 1969) have been determined.

Chicken and turkey lysozymes differ by at least seven amino acid substitutions,

chicken and *Coturnix* differ by at least six, and turkey differs from *Coturnix* by ten. Because some portions of the sequence are tentative, these may not be exact figures, but they suggest a closer relationship between *Gallus* and *Coturnix* than between *Coturnix* and *Meleagris*.

SUMMARY

Although many non-passerine taxa have been suggested as relatives of the Galliformes, the following have been proposed most frequently: Tinamidae, Anseriformes, Columbiformes, Turnicidae, and Thinocoridae.

The resemblances between tinamous and gallinaceous birds may be due to convergence, but there are enough similarities so that this question must receive careful consideration. The Anseriformes have been linked to the Galliformes primarily because the screamers (Anhimidae) resemble the galliforms in general appearance and some anatomical characters. Whether these groups are closely related is unknown. A relationship between the Columbiformes and Galliformes has been proposed because the sandgrouse (Pteroclididae), thought by many to be columbiform, share some features with the gallinaceous birds.

THE EGG WHITE PROTEIN EVIDENCE

ORDER GALLIFORMES

FAMILY MEGAPODIIDAE, Megapodes or Brush Turkeys. 4/18, fig. 16.

Species examined: *Megapodius freycinet*; *Leipoa ocellata*; *Alectura lathamii*; *Talegalla jobiensis*.

FAMILY CRACIDAE, Curassows, Guans, Chalchalacas. 5/37, fig. 16.

Species examined (nomenclature follows Vuilleumier, 1965): *Ortalis canicollis*; *Penelope superciliaris*; *Crax rubra*, *blumenbachii*, *mitu*.

FAMILY PHASIANIDAE

SUBFAMILY TETRAONINAE, Grouse. 9/16, fig. 16.

Species examined (nomenclature follows Short, 1967): *Dendragapus canadensis*, *obscurus*; *Lagopus lagopus*, *mutus*, *leucurus*; *Tetrao urogallus*; *Bonasa umbellus*; *Centrocercus urophasianus*; *Tympanuchus phasianellus*.

SUBFAMILY PHASIANINAE, Pheasants, Quail, Peafowl. 20/47, figs. 16, 17.

Species examined (nomenclature follows Delacour, 1951a): *Tragopan temmincki*, *caboti*; *Pucrasia macrolopha*; *Lophophorus impeyanus*; *Gallus gallus*, *sonnerati*; *Lophura nycthemera*, *swinhoei*, *diardi*; *Crossoptilon auritum*; *Syrnaticus ellioti*, *mikado*, *reevesi*; *Phasianus colchicus*, *versicolor*; *Chrysolophus pictus*, *amherstiae*; *Polyplectron bicalcaratum*, *malacense*; *Pavo cristatus*.

SUBFAMILY PERDIGINAE, Old World Quails. 11/98, fig. 17.

Species examined: *Alectoris graeca*, *rufa*, *barbara*; *Francolinus erckelii*; *Pternistis swainsonii*; *Perdix perdix*; *Melanoperdix nigra*; *Coturnix coturnix*; *Excalfactoria chinensis*; *Tropicoperdix charltonii*; *Rollulus roulroul*.

SUBFAMILY ODONTOPHORINAE, New World Quails. 6/36, figs. 17, 18.

Species examined: *Oreortyx picta*; *Callipepla squamata*; *Lophortyx californica*, *gambelii*, *douglasii*; *Colinus virginianus*.

SUBFAMILY NUMIDINAE, Guinea fowl. 2/7, fig. 18.

Species examined: *Numida meleagris*; *Guttera edouardi*.

SUBFAMILY MELEAGRIDINAE, Turkeys. 2/2, fig. 18.

Species examined: *Meleagris gallopavo*, *ocellata*.

The egg white proteins of all of the Galliformes studied by paper electrophoresis (Sibley, 1960) and starch gel electrophoresis have a distinctive pattern, but there are small differences in the mobilities of components. Usually there are three bands in the ovalbumin region. In fresh samples these bands are elliptical or biconvex in shape and sharply defined. The conalbumins appear as one or two dense bands migrating ahead of Component 18. There is an ovomucoid of varying concentration and there may be some minor bands between the conalbumins and ovalbumins. Most species possess a distinct lysozyme, which migrates cathodally. These features are illustrated best by the patterns of *Chrysolophus pictus* and *Colinus virginianus*.

The patterns of the Megapodiidae (e.g., *Alectura lathamii*) differ most from this description; Component 18 remains near the application point (in the phasianids it is usually halfway between the application point and the conalbumins), the overall length of the pattern is shorter, the conalbumins and ovalbumins are close together, and the ovalbumin region shows at least five components.

Within the Phasianidae the variation in the mobilities of some components is difficult to interpret. For example, the ability to hybridize (A. Gray, 1958) indicates a close relationship between *Phasianus colchicus* and *Chrysolophus pictus*, yet their egg white patterns show mobility differences in the conalbumins and ovalbumins. C. Baker (1965: fig. 1), using several different buffer systems, found similar variation among the patterns of 15 galliform species. As discussed in the Introduction, mobility differences may be an expression of genetic polymorphism within a species, or an artifact caused by differential binding of buffer ions. If total pattern and number of components, rather than mobility shifts, are considered, then *Bonasa*, *Lagopus*, *Numida*, and *Meleagris* fall within the limits of variation shown by typical phasianine patterns.

The egg white patterns of *Colinus virginianus* and *Lophortyx californicus* are nearly identical and differ little from those of other phasianids.

The egg white pattern of *Coturnix* closely resembles that of *Phasianus* and other genera of phasianids, thus conflicting with the conclusions based on osteology, immunological cross-reactivity, and appendicular myology.

The pattern of *Perdix* differs in having slower mobilities of all components, particularly the ovalbumins. The arrangement and concentrations of the components are like those of other gallinaceous birds. Sibley (1960) also noted this "short" pattern of *Perdix* in paper electrophoretic analyses. It seems likely that a charge difference on the ovalbumin molecule is responsible for this compressed but otherwise typical gallinaceous pattern. No author has challenged a close relationship between *Perdix* and other Phasianidae.

The egg white patterns of the chachalaca *Ortalis* and guan *Penelope* fall within the variation of phasianid patterns. They do not show the multiple subdivision of the ovalbumin region which is characteristic of megapodes, and they differ from the megapodes in other areas of the pattern. This evidence conflicts with a number of opinions but agrees with Sibley's (1960) observation. Mainardi and Taibel (1962) and H. Clark (1964a) also did not favor a close megapode-cracid alliance.

There is little in the egg white evidence to suggest a relationship of the Galliformes to other avian orders. The features of the ovalbumin region resemble the corresponding part of the tinamou pattern, but the similarity ends there. The Turnicidae, Thinocoridae, and Pteroclididae, all of which have been suggested as possible relatives of the Galliformes, have considerably different patterns.

CONCLUSIONS

The egg white data agree with the evidence from osteology, immunology, hemoglobins and hybridization that the species of Phasianidae are closely related. The egg white patterns alone cannot be used to postulate relationships among the phasianid genera, and additional biochemical studies are necessary. The Cracidae perhaps deserve only subfamily rank within the Phasianidae. They do, however, have a number of structural peculiarities, some of which may be correlated with their arboreal way of life. A careful study of the relationships of the cracids to the phasianids needs to be undertaken. The megapodes are distinctive in many points and may be left as a separate family in the Galliformes.

ORDER GRUIFORMES

-
- Suborder Mesitornithides
 - Family Mesitornithidae, Roatelos, Monias
 - Suborder Turnices
 - Family Turnicidae, Bustardquails
 - Family Pedionomidae, Plains-wanderers
 - Suborder Grues
 - Superfamily Gruoidea
 - Family Gruidae, Cranes
 - Family Aramidae, Limpkins
 - Family Psophiidae, Trumpeters
 - Superfamily Ralloidea
 - Family Rallidae, Rails, Coots, Gallinules
 - Suborder Heliornithes
 - Family Heliornithidae, Sungrebes
 - Suborder Rhynocheti
 - Family Rhynochetidae, Kagus
 - Suborder Eurypygae
 - Family Eurypygidae, Sunbitterns
 - Suborder Cariamae
 - Superfamily Cariamoidea
 - Family Cariamidae, Seriemas
 - Suborder Otides
 - Family Otididae, Bustards

Wetmore, 1960

INTRODUCTION

The living species of the order Gruiformes as defined by Wetmore (1960) have been arranged by him in 8 suborders and 12 families. E. Stresemann (1927-34) placed the same species in 10 separate orders. These two treatments illustrate the exceptional disparity of opinion about the classification of this heterogeneous assemblage. The

unusual variation among the groups is also evident in the diagnoses presented by Ridgway and Friedmann (1941), Gadow (1893) and others. The morphological diversity of the subgroups included in the Gruiformes by Wetmore makes the order virtually impossible to define. We have therefore summarized the principal anatomical characters of each of the 12 families in Table 2.

The relationships of each family to the other gruiforms and to other orders pose an exceptionally large number of questions. The literature is correspondingly complex and extensive. The Gruidae, Aramidae, Psophiidae and Rallidae are generally thought to constitute a core group, with the other eight families viewed as satellites of uncertain relation to the core. The Galliformes and Charadriiformes are most frequently mentioned as possible relatives of the Gruiformes but several other orders have also been proposed as relatives of one or more of the gruiform families.

In the following review of the literature we use the words "gruiform" and "Gruiformes", unless otherwise specified, to mean those birds included in the order Gruiformes by Wetmore (1960) and Peters (1934).

HISTORICAL REVIEW OF THE CLASSIFICATION

Early systematists assigned the presently recognized subgroups of the Gruiformes to a variety of higher categories. For example, Linnaeus (1758) placed *Otis* with the ratites, and the same or a similar arrangement was also followed by Illiger (1811), Vieillot (1816), Cuvier (1817, 1827-35) and Temminck (1820-40). The same authors thought that the cranes are related to the herons and that *Turnix* is allied to the gallinaceous birds. Illiger (1811) proposed an alliance among *Fulica*, *Podica*, and *Phalaropus*, and Temminck (1820-40) placed *Fulica*, *Phalaropus*, and *Podiceps* in the same "order." Both systems were based on foot structure. It is obvious that these assignments were founded on convergent similarities. Several other pre-Darwinian authors were more successful in discerning evidence of common ancestry. For example, Merrem (1813) recognized similarities between *Rallus* and *Fulica* and between *Grus* and *Psophia*. Cuvier (1817) associated *Psophia* with the cranes and considered *Aramus* and *Eurypyga* (as well as *Cochlearius*) intermediate between cranes and herons. L'Herminier (1827) described osteological similarities between cranes and rails and concluded that neither group is close to the herons. Lesson (1831) placed *Otis* near *Psophia*. W. Martin (1836) found *Cariama* crane-like in general organization and noted similarities to *Psophia* in its visceral anatomy.

The Alectorides of Nitzsch (1840) contained *Palamedea* (= *Anhima*), *Otis*, *Dicholophus* (= *Cariama*), *Psophia*, and *Grus*, an admittedly heterogenous assemblage. He found that the pterylosis of *Aramus* differs little from that of *Psophia* and *Grus*, but because of the rail-like appearance of the bill and feet he placed *Aramus* in his Fulicariae along with rails, jacanas, and sungrebes (*Heliornithidae*). The Fulicariae of Giebel (1861) also included the *Heliornithidae*, but Schlegel (1867) united *Heliornis* with *Spheniscus*, *Alca*, *Podiceps*, and *Colymbus* (= *Gavia*) in his *Urinatores*.

G. Gray (1844-49) placed the Turnicidae in the Tetraonidae and made the Otididae a subfamily of the Struthionidae. He thought that *Psophia* and the cranes belonged in the Ardeidae. He put the Rallidae next to the Anhimidae and Jacanidae.

In describing *Rhynochetos*, Verreaux and Des Murs (1860) were impressed by the heron-like aspects of its plumage and color pattern. A. Bartlett (1861) placed *Eurypyga*, along with *Balaeniceps* and *Cochlearius*, in the Ardeidae because all possess powder downs. He (1862) found resemblances between *Rhynochetos* and *Eurypyga*

TABLE 2. Principal anatomical characters of Gruiformes

	PALATE TYPE	MUSCLE FORMULA	UROPYGIAL GLAND	INTESTINAL COILING
Mesitornithidae	Schizognathous ^{bb,cc}	ABXY+ ^{bb,cc,dd}	Nude ^f Tufted ^e None ⁿⁿ	Plagiocoelus ^{ff}
Turnicidae	Aegithognathous ^{kk} Schizognathous ^a	AXY+ ^g	Tufted ^{tt}	Plagiocoelus ^l
Pedionomidae	Aegithognathous ^{kk}	ABXY+ ^k	Tufted ^k	Plagiocoelus ^l
Gruidae	Schizognathous ^g	ABDXY+ V ^y ABXY+ ^a exc. BXY+ (<i>Balearica</i>), ^a XY+ (<i>Grus leucogeranus</i>) ^o	Tufted ^l	Pericoelus ^{hh,j}
Aramidae	Schizognathous ^t	BXY+ ^t	Tufted ^l	Pericoelus ⁿ
Psophiidae	Schizognathous ^g	BXY+ ^g	Tufted ^l	Pericoelus ⁿ
Rallidae	Schizognathous ^g	ABDXY+V ^y	Tufted, exc. nude in <i>Himantornis</i> , ⁿⁿ	Pericoelus ^{hh,j}
Heliornithidae	Schizognathous ^g	ABX+ ^p	Tufted ^l	Modified pericoelus ^j
Rhynochetidae	Schizognathous ^g Dromeognathous tendency ^l	AXY+ ^a	Nude ^{hh} Tufted ^e	Modified pericoelus like <i>Heliornis</i> ^j
Eurypygidae	Schizognathous ^g	AXY+ ^g	Nude ^e Tufted ^{hh}	Pericoelus ^{ff}
Cariamidae	Schizognathous ^g Desmognathous ^{kk}	BXY (<i>Cariama</i>) ^a ; XY+ ^a and BXY+ ^c in <i>Chunga</i>	Nude ^a	Pericoelus ⁿ
Otididae	Schizognathous ^g	BXY+ ^a	None ^{mm}	Pericoelus ⁿ

TABLE 2 (continued)

	STERNAL NOTCHES	SUPRA- ORBITAL FURROWS	NO. OF CERVICAL VERTEBRAE	BASIPTERYGOID PROCESSES	CAROTID ARTERIES
Mesitornithidae	one ^{mm}	Absent ^m	17 ⁿⁿ	Absent ^{ee}	A-1 ^w
Turnicidae	one ^{ll}	Absent ^m	15 ^e	Present ^z	B-4-s ^q
Pedionomidae	one ^k	Absent ^m	15 ^k	Present ^f	A-1 ^{oo}
Gruidae	none ^{mm}	Present ^{mm}	19-20 ^g	Absent, exc. in <i>Grus antigone</i> ^z & <i>Anthropoides</i> ^{aa}	A-1 ^u
Aramidae	none ^{mm}	Absent ^m	17 ⁿⁿ	Absent ^f	A-1 ^w
Psophiidae	none ⁿⁿ	Absent ^m	17-18 ^g	Absent ^z	A-1 ^w
Rallidae	one ^{jj}	Present ^m Absent ^m	14-15 ^g	Absent ^z	A-1 ^q
Heliornithidae	one ^{mm}	Absent ^{mm}	15-16 ⁿⁿ	Absent ^g	B-4-s ^x
Rhynchotidae	none ^l	Absent ^{mm}	16 ⁿⁿ	Absent ^z	A-1 ^v
Eurypygidae	one ^{mm}	Absent ^{mm}	18 ⁿⁿ	Absent ^z	A-1 ^w
Cariamidae	one ⁿⁿ	Absent ^m	15 ⁿⁿ	Absent ^z	A-1 ^q
Otididae	two ^{mm}	Absent ^m	16-18 ⁿⁿ	Absent, exc. in <i>Chlamydotis undulata</i> ^{aa,pp}	A-1, exc. B-4-d in <i>Eupodotis</i> , B-4-s in <i>Tetrax</i> ^{q,r,w}

TABLE 2 (continued)

	HALLUX	FLEXOR TENDONS	NOSTRILS	NARES
Mesitornithidae	Present; elevated ¹	Type I ^a	Schizorhinal ^f	Pervious ^m
Turnicidae	Absent ¹	Type IV ^a	Schizorhinal ^g	Impervious ^m
Pedionomidae	Present ^k	Type IV ^k	Schizorhinal ^k	Impervious ^k
Gruidae	Small, elevated ¹	Type I ^a	Schizorhinal ^g	Pervious ^m
Aramidae	Large, incumbent ¹	Type I ^a	Schizorhinal ^l	Pervious ^m
Psophiidae	Present; small ¹	Type I ^a	Holorhinal ^g	Pervious ^m
Rallidae	Nearly incumbent ¹	Type I ^a	Holorhinal ^g exc. <i>Nesolimnas</i> ^m	Pervious ^m
Heliornithidae	Incumbent ¹	Type II ^a	Holorhinal ^d	Pervious ^m
Rhynchoetidae	Present ¹	Type I ^a	Schizorhinal ^g	Impervious ^m
Eurypygidae	Incumbent ¹	Type I ^a	Schizorhinal ^g	Pervious ^m
Cariamidae	Small, elevated ¹	Type IV ^a	Holorhinal ^g	Pervious ^m
Otididae	Absent ¹	Type I ^a	Holorhinal ^g	Pervious ^m

TABLE 2 (continued)

	NO. OF PRIMARIES	NO. OF RETRICES	AFTERSHAFT	FIFTH SECONDARY	POWDER DOWNS
Mesitornithidae	10 ^{mn}	16 ^f	Present ^e	Eutaxic ^{mn}	5 prs. ^b present
Turnicidae	10 ⁿⁿ	12 ^e	Present ^e	Eutaxic ^{ll}	Absent ^g
Pedionomidae	10 ^k	12 ^k	Present ^{kt}	Diastataxic ^k	Absent ^g
Gruidae	11, 10 in Balearica ⁿⁿ	12 ^g	Present ^e	Diastataxic ^l	Absent ^g
Aramidae	10 ^{gg} 11 ^m	12 ^g	Present ^e	Diastataxic ^l	Absent ^g
Psophiidae	10 ⁿⁿ	12 ^g	Present ^e	Eutaxic ^l	Absent ^g
Rallidae	10 or 11, rarely 8 or 9 ⁿⁿ	12 ⁿⁿ	Present ^{mm}	Diastataxic, exc. eutaxic in <i>Himantornis</i> , <i>Amaurolimnas</i> ⁿⁿ	Absent ^g
Heliornithidae	10 ⁿⁿ	18 ^{mm}	Absent exc. in <i>Podica</i> ⁿⁿ	Diastataxic ^m	Absent ^g
Rhynochetidae	10 ^{hh}	12 ^g	Present ^{hh}	Eutaxic ^l	Diffuse ^a
Eurypygidae	10 ^{mm}	12 ^g	Present ^{hh}	Diastataxic ^l	Diffuse ^a
Cariamidae	10 ⁿⁿ	12 ^g	Present ^e	Eutaxic ^l	Absent ^g
Otididae	11 ⁿⁿ	16-20 ⁿⁿ	Present ^{mm}	Diastataxic ^m	Absent ^g

^aA. Bartlett, 1862. ^bE. Bartlett, 1877. ^cBeddard, 1889d. ^dBeddard, 1890b. ^eBeddard, 1898a. ^fForbes, 1882b. ^gFürbringer, 1888. ^hGadow, 1879. ⁱGadow, 1888. ^jGadow, 1889. ^kGadow, 1891. ^lGadow, 1892. ^mGadow, 1893. ⁿGadow and Selenka, 1891. ^oGarrod, 1873a. ^pGarrod, 1873b. ^qGarrod, 1873d. ^rGarrod, 1874c. ^sGarrod, 1875. ^tGarrod, 1876c. ^uGlenny, 1945b. ^vGlenny, 1947b. ^wGlenny, 1955. ^xGlenny, 1967. ^yHudson, 1937. ^zHuxley, 1867. ^{aa}Lowe, 1931a. ^{bb}Milne-Edwards, 1878a. ^{cc}Milne-Edwards, 1878b. ^{dd}Milne-Edwards and Grandidier, 1879. ^{ee}Milne-Edwards and Grandidier, 1881. ^{ff}Mitchell, 1901b. ^{gg}Mitchell, 1915. ^{hh}Murie, 1871. ⁱⁱOgilvie-Grant, 1893. ^{jj}Owen, 1882. ^{kk}Parker, 1875a. ^{ll}P. Sclater, 1890. ^{mm}Sharpe, 1894. ⁿⁿE. Stresemann, 1927-34. ^{oo}Wetmore, 1951. ^{pp}(= *Otis houbara* of Lowe).

in wing and tail markings and in the method of spreading the wings during display. He also found (1866) that the eggs of *Rhynochetos* are blotched like those of *Eurypyga* and the cranes rather than unmarked like those of a heron.

The Geranomorphae of Huxley (1867) included the cranes and rails with *Psophia* and *Rhynochetos* as intermediate forms. The Otididae, in Huxley's opinion, connect the cranes with the plovers, while the Cariamidae are distantly allied to the diurnal birds of prey. He concluded that the Turnicidae should be maintained as a separate group, and noted (p. 304) that "the chief relations of *Hemipodius* [= *Turnix*] are on one hand with *Tinamus*, on another with *Syrhaptēs*, and on a third with the plovers, *Pedionomus* being perhaps the connecting link between the latter and it."

Parker (1868: 158) decided on osteological grounds that "the bustards are gigantic plovers." Sundevall (1872) placed *Mesitornis* among the Oscines. Murie (1871) concluded from a study of myology and osteology that *Rhynochetos* is closer to *Eurypyga* than either is to *Cochlearius*.

On the basis of pelvic musculature Garrod (1873d, 1874a) considered the Rallidae and Otididae to be allied. *Burhinus*, *Sagittarius*, *Cariama*, and the bustards composed his Otididae. He placed the Gruidae between the Charadriidae and Laridae. *Aramus* "is most intimately related to *Grus*, which, with it, is not distant from *Ibis*, *Platalea*, and *Eurypyga*" (1876c: 275).

To E. Bartlett (1877) the Mesitornithidae were strikingly similar to the Eurypygidae. Milne-Edwards (1878a,b) found resemblances to the Rallidae and to *Eurypyga* chiefly in the skeleton, but Forbes (1882b) thought that the mesitornithids were anatomically most like the Eurypygidae and Rhynochetidae and not close to the Rallidae.

Stejneger (1885: 122) thought that the Psophiidae are "evidently related to the kagu and seriema, and likewise in their structure exhibiting characters to a certain degree uniting rails and cranes. . . ." *Aramus* is "completely intermediate between cranes and rails, making their separation into different sub-orders indefensible" (p. 127). The Turnicidae inadvertently were omitted from the text of the work, although *Turnix sylvatica* is figured with *Coturnix communis* opposite page 198 in the section on the Gallinae.

Goodchild (1886) found that the arrangement of the secondary coverts in *Cariama* is like that of the bustards and differs from that of *Sagittarius*. This arrangement is also shared by the Burhinidae, Charadriidae, Scolopacidae, Gaviidae, Alcidae, and Gruidae (1891).

The Gruiformes are connected with the Charadriiformes by *Eurypyga* and with the Ralliformes by *Aramus*, according to Fürbringer (1888). In his opinion, *Cariama* is a highly specialized gruiform, only convergently similar to the birds of prey. He believed that the Ralliformes are distantly allied to the Tinamidae and *Apteryx* through the Turnicidae.

Beddard (1890a) contended that *Psophia* and *Cariama* share the largest number of characters. The next closest ally of *Psophia*, he thought, is *Burhinus* (Charadriiformes) followed by the Gruidae. He (1890b, 1893) also studied the anatomy of the Heliornithidae, and found that their myology is most like that of the loons and grebes, although their osteology resembles that of rails. "The Heliornithidae form a distinct family which has traversed for a certain distance the branch leading from the Rails to the Colymbidae [= loons] and has then diverged rather widely in a direction of its own" (1890b: 442).

Sharpe (1891) decided that *Aramus* is intermediate between cranes and rails and that the trumpeters are the "most Galline of all the Crane-like birds" (p. 63). Like Huxley (1867) he considered the cariamas to be a link between cranes and the diurnal birds of prey.

In his Galliformes Gadow (1893) included the Mesitornithidae, Turnicidae, and Pedionomidae. He felt that *Aramus* and *Psophia* deserve only subfamily rank within the Gruidae and that the nearest relative of *Cariama* is *Psophia*, followed by *Rhynochetos* and *Eurypyga*. In his opinion, the bustards, although gruiform, stand alone with no obvious close relatives. Their resemblance to the Burhinidae was attributed to convergence.

Beddard (1898a) was so impressed by the similarities between Gruiformes and Charadriiformes that he stated (p. 358): "The very difficulty of finding any characters, greatly noteworthy, in which the groups in question [Limicolae, Grues, Otides, Ralli] vary is an index of how closely allied all four are. There can, to my mind, be no doubt of their common origin. The Limicolae on the whole come nearest to the Grues, and especially to the true cranes. . . ."

Mitchell (1901a) found that all gruiform families except the Turnicidae and Mesitornithidae have a similar pattern of intestinal coiling. This is like that of the Charadriiformes. In Mitchell's opinion, the Rallidae, Aramidae, Gruidae, Otididae and Eurypygidae have more primitive characters of the alimentary tract than do the Psophiidae, Cariamidae, Rhynochetidae, and Heliornithidae.

From osteological characters Shufeldt (1894b) concluded that *Aramus* is intermediate between cranes and rails. He united the three groups in the same superfamily. On the basis of similar evidence Beddard (1902a) argued that *Aramus* should be placed in the same subfamily as the cranes. In later papers Shufeldt (1904b, 1915a) disagreed with Beddard and placed *Aramus*, the Rallidae, and the Heliornithidae in his "supersuborder" Ralliformes. (Shufeldt's "supersuborder" is equivalent to a suborder of Fürbringer or an order of Wetmore.) Mitchell (1915) enumerated several characters of the skull of *Aramus* that are "exceedingly like those of cranes," and Shufeldt (1915b) also changed his opinion and ranked *Aramus*, the cranes, and the trumpeters as separate families within his Gruoidea.

Beddard (1910) wrote that the alimentary tract of the Turnicidae is unlike that of gallinaceous birds and most similar to that of passerines. He also pointed out that the bustards *Eupodotis australis* and *Houbara macqueeni* (= *Chlamydotis undulata*) are nearly identical to *Chunga burmeisteri* in their pattern of intestinal coilings, but neither group is especially similar to the cranes.

L. Harrison (1915) found similarities between the Mallophaga of rails and those of *Apteryx*.

To Chandler (1916) the structure of the feathers of the Rallidae indicated "striking affinity" to the Charadriiformes. The Gruidae agree in some points with the storks and in others with the shore birds. *Aramus* is intermediate between cranes and rails in the structure of its breast feathers, but its back feathers resemble those of the Cracidae and Megapodiidae. Chandler reasoned that the Gruidae, Aramidae, and Rallidae evolved from the stem leading to the Charadriiformes. *Psophia* and *Otis* share a number of features with the gallinaceous birds, and Chandler thought them to be early offshoots of a line ancestral to the Galliformes and Columbiformes. *Eurypyga* and, to a lesser degree, *Cariama* resemble the Ciconiiformes in some aspects of their feather structure, and are "almost certainly of ardeid derivation" (p. 354).

Lowe (1923: 277) regarded the Turnicidae, along with the Pteroclididae and Thinocoridae, "as the still-surviving blind-alley offshoots of an ancient generalized and basal group (now extinct), from which group sprang the now dominant Plovers, Pigeons, and Fowls." He studied the osteology, myology, and pterylosis of *Mesitornis*, "a primitive form of arboreal rail" with a "decided tendency to Gruiform relationships" (1924: 1151). He thought that the Mesitornithidae were best retained as a separate order. Lowe (1931a) examined the anatomical evidence for relationships among the Gruiformes and Charadriiformes. On the basis of a "less specialized"

structure of the contour feathers he erected the order Ralliformes for the Rallidae and Heliornithidae. Of the remaining gruiform groups he observed (p. 496): "... They seem to me to be neither distinct enough from the Charadriiformes, nor to agree enough among themselves in any outstanding character or characters, to justify their separation as an isolated order." After emphasizing the similarities among these groups in myology, intestinal tract, and pterylosis, Lowe pointed out 11 osteological differences, none of which, however, "differs to such a degree that it ought to stand in rank as an ordinal character" (p. 501). Thus, he combined gruiform and charadriiform birds into a single order Telmatomorphae, defined by the following characters:

- 1) Dorsal feather tract forked and characteristically separated into dorsal and posterior portions.
- 2) Vomer anchored posteriorly to ethmo-palatine laminae.
- 3) Oil gland tufted.
- 4) Characteristic down structure in chicks (to exclude Columbiformes).
- 5) Barbules of basal third of contour feathers with plumaceous structure at their proximal end.
- 6) Caeca well developed.
- 7) Diastataxic.
- 8) Palatines with internal laminae present.
- 9) Nostrils not tubular (to exclude Procellariiformes).
- 10) Recurrent slip to tensor patagii longus muscles.

Lowe left the Cariamidae in an uncertain position because of their desmognathous palate. The "Turnicomorphs" and *Mesites* (= *Mesitornis*) are excluded from the Telmatomorphae by Lowe's list of defining characters. Apparently he thought that they should constitute separate orders.

E. Stresemann (1927-34) established 10 orders for 12 gruiform families, and in his linear sequence interposed other groups among them. The classification of Wetmore (1930) was the first to unite all 12 groups under consideration into a single order, an arrangement also followed by Peters (1934).

The following characters are shared by Gruiformes, Charadriiformes and Galliformes (Ridgway and Friedmann, 1941: 3):

- 1) Schizognathous palate (desmognathous in Cariamae and aegithognathous in Turnices).
- 2) Double head of quadrate.
- 3) Ilium and ischium united at their distal ends.
- 4) Absence of slip to accessory femorocaudal muscles.

The Gruiformes agree with the Charadriiformes, but differ from the Galliformes, in the following:

- 1) Basal ends of coracoids separated or merely touching.
- 2) Absence of spina interna sterni muscle.
- 3) Intestinal convolutions of Type I instead of Type V.

The Gruiformes differ from the Charadriiformes as follows:

- 1) Heterocoelus (instead of opisthocoelus) dorsal vertebrae.
- 2) Absence of basipterygoid processes.

Ridgway and Friedmann concluded that the Gruiformes "are related on the one hand to the Charadriiformes and on the other to the Galliformes, occupying . . . a position somewhat intermediate between these two. It is not, however, a homogeneous group, and it is doubtful whether the Cariamae and Heliornithes, at least, should not be excluded" (p. 3).

The fossil evidence persuaded Howard (1950) to agree with Lowe (1931a) on the common ancestry of the Gruiformes and Charadriiformes. She emphasized that no gruiform or charadriiform groups can be recognized until the Eocene.

Hopkins (1942) stated that the Mallophaga indicate that the bustards (Otididae) "do not belong to the Gruiformes" (p. 104) and that he would not be surprised if the bustards should prove to be related to the Galliformes. He discounted even a distant relationship between bustards and the Charadriiformes.

Evidence from the Mallophaga bearing on gruiform relationships was presented by Clay (1950, 1953). Of five genera of Mallophaga found on rails three are also found on *Aramus* and two on *Psophia*. Some genera of the ralline mallophagan fauna also have been reported from the Heliornithidae and from *Rhynochetos*, but the four genera found on cranes are shared by none of these groups. One genus of Mallophaga found on bustards appears to have its nearest relatives on gallinaceous birds and the Scolopacidae. The mallophagan genera parasitizing Mesitornithidae and Turnicidae are related. The Mallophaga of *Eurypyga* are uninformative in this regard. Two genera on the Cariamidae occur also on tinamous, a probable secondary infestation on the cariamias.

Verheyen (1957b-d; 1958a) concluded from an osteological study that the Gruiformes of Peters (1934) are an artificial assemblage and proposed four separate orders for them:

- 1) Ralliformes, with suborders Otides, Psophiae, Grues (Gruidae, Aramididae), and Ralli (Rallidae, Heliornithidae)
- 2) Cariamiformes (Cariamidae, *Sagittarius*)
- 3) Jacaniformes (Rhynochetidae, Eurypygidae, Jacanidae)
- 4) Turniciformes, with suborders Mesoenatidae, Turnices, Pterocletes (Thino-coridae, Pteroclididae).

Verheyen (1959) included the grebes in his Ralliformes because of similarities to the Heliornithidae. In his final classification (1961), Verheyen made other changes. The Ralliformes now included only the Rallidae and Heliornithidae, and he split his earlier order Turniciformes by placing the Mesitornithidae as a suborder of the Jacaniformes. He allocated the Turnicidae and Pedionomidae to a suborder of the Galliformes, and transferred *Sagittarius* from the Cariamiformes to the Falconiformes. In this arrangement Verheyen placed the Struthioniformes, Galliformes, Gruiformes, and Cariamiformes in a superorder, Chamaeornithes, while the Jacaniformes and Ralliformes are members of the superorder Limnornithes.

The egg white protein pattern of *Aramus* in paper electrophoresis is more like those of rails than those of cranes (Sibley, 1960). The pattern of *Psophia* seems to be intermediate between those of the Rallidae and Gruidae. Sibley also noted some resemblances between the patterns of rails and of Charadriiformes and Galliformes.

The egg white patterns of gruiform birds in starch gel electrophoresis were compared by Hendrickson (1969). The pattern of *Aramus* is intermediate between those of cranes and rails and the patterns of the Turnicidae, the finfoot *Heliopais*, *Psophia*, and *Eurypyga* are most like those of rails. The patterns of *Rhynochetos*, the Cariamidae, and the Otididae differ from those of the rails and from one another.

The arteries in the neck and thorax of the sungrebes (Heliornithidae) were studied by Glenny (1967). *Podica* and *Heliornis* have the B-4-s carotid pattern which is shared with the Turnicidae and some Otididae. Other Gruiformes have the A-1 carotid arrangement.

Cracraft (1968) reviewed the fossil family Bathornithidae and hypothesized that they were related to the Cariamidae and Phororhacidae of the gruiform suborder Cariamae.

Bock and McEvey (1969a) found that *Pedionomus* is fairly distinct osteologically from the Turnicidae and they supported the maintenance of the two groups in separate families. They also recognized both *Turnix* and *Ortyxelos* as distinct genera within the Turnicidae.

SUMMARY

There is little consensus regarding the relationships among the families of the Gruiformes. A frequently proposed assemblage is that of the Gruidae, Aramidae, and Rallidae, with *Aramus* in an intermediate position. However, similarities between the cranes and the storks also have been found. *Aramus* has been thought to be related to the shore birds, the gallinaceous birds, and the herons. The shorebirds, Tinamidae, and Apterygidae have also been suggested as more distant relatives of the rails. *Psophia* has usually been considered to be on the periphery of a crane-*Aramus*-rail group, but resemblances to the gallinaceous birds have also been noted. The Heliornithidae often have been placed near the Rallidae, but a relationship to the grebes has also been proposed. The Cariamidae have been thought to be related to the diurnal birds of prey (especially *Sagittarius*) as well as to various gruiform groups, especially *Psophia*. The Otididae have been placed among the gruiform birds, near the Burhinidae, and next to the ratites. Some of these allocations are clearly influenced by convergent similarities. Although both *Eurypyga* and *Rhynochetos* have been considered to be closely related to the Ardeidae, they may be most closely allied to each other or to some other gruiform group. The Turnicidae and *Pedionomus* have usually been thought to be allied to one another, but their proposed relatives have included the Rallidae, Pteroclididae, and the Galliformes. The Mesitornithidae have been considered to be oscine, galliform or ralline.

THE EGG WHITE PROTEIN EVIDENCE

ORDER GRUIFORMES

FAMILY MESITORNITHIDAE, Roatelos, Monias, Mesites. 0/3.

FAMILY TURNICIDAE, Bustardquails. 4/15, fig. 18.

Species examined: *Turnix sylvatica*, *melanogaster*, *varia*, *velox*.

FAMILY PEDIONOMIDAE, Plains-wanderers or Collared Hemipodes. 0/1.

FAMILY GRUIDAE, Cranes. 4/14, fig. 18.

Species examined: *Grus grus*, *canadensis*, *rubicunda*; *Balearica pavonina*.

FAMILY ARAMIDAE, Limpkins. 1/1, fig. 18.

Species examined: *Aramus guarauna*.

FAMILY PSOPHIDAE, Trumpeters. 2/3, fig. 18.

Species examined: *Psophia crepitans*, *leucoptera*.

FAMILY RALLIDAE, Rails, Coots, Gallinules. 38/132, figs. 18, 19.

Species examined: *Rallus longirostris*, *limicola*, *aquaticus*, *caerulescens*, *striatus*, *philippensis*; *Ortygonax rytirhynchos*; *Rallina fasciata*; *Aramides cajanea*; *Crecoptis egregia*; *Limnocorax flavirostra*; *Porzana parva*, *pusilla*, *carolina*, *albicollis*, *fusca*; *Laterallus jamaicensis*, *albigularis*, *melanophaius*; *Neocrex erythrops*; *Sarothrura rufa*, *elegans*, *affinis*; *Poliolimnas cinereus*; *Porphyriops melanops*; *Amaurornis phoenicurus*; *Gallinula tenebrosa*, *chloropus*; *Porphyriops martinica*; *Porphyrio porphyrio*, *madagascariensis*, *albus*; *Notornis mantelli*; *Fulica atra*, *cristata*, *armillata*, *leucoptera*, *cornuta*.

FAMILY HELIORNITHIDAE, Sungrebes or Finfoots. 1/3.

Species examined: *Heliopais personata*.

FAMILY RHYNOCHETIDAE, Kagu. 1/1, fig. 19.

Species examined: *Rhynochetos jubatus*.

FAMILY EURYPYGIDAE, Sunbittern. 1/1, fig. 20.

Species examined: *Eurypyga helias*.

FAMILY CARIAMIDAE, Cariamias or Seriemas. 2/2, fig. 20.

Species examined: *Cariama cristata*; *Chunga burmeisteri*.

FAMILY OTIDIDAE, Bustards. 4/23, fig. 20.

Species examined: *Otis tarda*; *Choriotis kori*; *Afrotis atra*; *Lissotis melanogaster*.

Our starch gel evidence largely corroborates the observations of Hendrickson (1969).

The egg white patterns of all Rallidae examined are similar to one another. The ovalbumin region is composed of three bands, the most concentrated one being in the middle. (See, e.g., the pattern of *Limnocorax flavirostra*.) In *Fulica cristata* the two anodal components of ovalbumin are close together. The patterns from older samples tend to have the two anodal bands merged together and show the third as "tailing" (see *Rallus limicola* and *Gallinula chloropus*). Cathodal to the ovalbumin is the ovomucoid, usually not well defined. It may be present in low concentration as in *Aramides cajanea*.

There is a general resemblance between the patterns of rails and those of the Charadriiformes. The main difference is in the ovalbumin region which, in most shorebirds, is a single band, but in some (e.g., the Rostratulidae, Recurvirostridae, and Burhinidae) there are two components, the more anodal being the smaller. A resemblance between the rail patterns and those of gallinaceous birds, tinamous, and *Apteryx* is seen in the tripartite ovalbumin region but the mobilities differ.

Aramus agrees with the rails in the shape and mobility of the ovalbumin, but the conalbumins have a position between that of most rails and that of the crane *Balearica*. The Rallidae have conalbumins migrating between the application point and Component 18, whereas in *Aramus* and *Balearica* they move anodal to Component 18. In *Balearica* there appear to be the same indistinct bands behind the ovalbumin region, but they are not well resolved in this older sample. An ovomucoid cannot be identified with certainty in *Balearica*, but presumably it is present. In the position of the ovomucoid *Aramus* resembles *Rallus limicola*, *Amaurornis*, *Fulica*, and *Gallinula*.

The pattern of *Psophia* is identical and resembles those of the Rallidae in both the positions and shapes of the ovalbumin and the ovotransferrins. (Compare with *Rallus* and *Poliolimnas cinereus*.) *Psophia* differs slightly in having a more concentrated ovomucoid than many rails (but see *Fulica* and *Gallinula*) and a thin prealbumin, not generally observed in rail patterns. Similarities to *Balearica* are less striking.

The egg white pattern of *Eurypyga* agrees with those of the rails and *Psophia* in most aspects. Component 18 in *Eurypyga* has a slower mobility and lower concentration than the Components 18 of rails, and the mobility of the ovomucoid is slightly less than that of *Psophia* or *Rallus*.

The patterns of the Turnicidae differ from those of the rails in minor points. The ovomucoid, which has a slower mobility, is not sharply defined and is subdivided. The ovotransferrins migrate ahead of Component 18. We cannot tell if there are three components in the ovalbumin, but the pattern of *Turnix varia* suggests that there is more than one. The patterns of the Turnicidae are unlike those of gallinaceous birds.

The pattern of *Cariama cristata* is based on poor material. It seems to resemble the rail pattern but differs in having a cathodally migrating component. The pattern differs somewhat from that of *Sagittarius*, but not enough to rule out the possibility of relationship.

The patterns of the Otididae do not resemble those of rails. The fast ovalbumin,

the absence of well-defined bands in the middle region of the pattern, and the presence of cathodally migrating components make the pattern superficially like those of ratites. Component 18 is apparently missing, and a prealbumin is present. The patterns of bustards do not resemble those of the Burhinidae. Some aspects of the bustard pattern suggest the patterns of the large ratites but the similarities are not great and there are differences.

The starch gel pattern of *Rhynochetos* features a large anodal component, which may be both the ovalbumin and ovomucoid together, and a faint series of conalbumins just off the application point. Component 18 seems to be absent. The mobility of the main anodal band is less than that in the rail pattern. The mobility of the ovalbumin of *Psophia* is approximately the same as that of the Rallidae, *Turnix*, and *Eurypyga*. The resemblances between the pattern of *Rhynochetos* and those of other Gruiformes are slight and comparisons to other avian groups reveal nothing of significance.

CONCLUSIONS

We conclude that the egg white protein patterns of the Rallidae, Aramidae, Gruidae, Heliornithidae, Psophiidae, Turnicidae and Eurypygidae are similar enough to suggest a relationship among these groups. The pattern of *Aramus* is more like those of rails than those of cranes, but since this single sample is partially denatured, the similarity is of little value in assessing relationships. The patterns of the Cariamidae may or may not fall within this group.

The patterns of bustards are not like those of the rail-crane group nor are they like those of the Burhinidae. We see a superficial resemblance between the patterns of the Otidae and those of the large ratites but this must be investigated by more detailed studies before its significance can be assessed. The egg white pattern of *Rhynochetos* is uninformative concerning possible relationships.

ORDER CHARADRIIFORMES

Suborder Charadrii

Superfamily Jacanoidea

Family Jacanidae, Jacanas

Superfamily Charadrioidae

Family Rostratulidae, Painted-Snipe

Family Haematopodidae, Oystercatchers

Family Charadriidae, Plovers, Turnstones, Surfbirds

Family Scolopacidae, Snipe, Woodcock, Sandpipers

Family Recurvirostridae, Avocets, Stilts

Family Phalaropodidae, Phalaropes

Superfamily Dromadoidea

Family Dromadidae, Crab-plovers

Superfamily Burhinoidea

Family Burhinidae, Thick-knees

Superfamily Glareoloidea

Family Glareolidae, Pratincoles, Coursers

Superfamily Thinocoroidea

Family Thinocoridae, Seedsnipe

Superfamily Chionioidea

Family Chionididae, Sheathbills

Suborder Lari

Family Stercorariidae, Skuas, Jaegers

Family Laridae, Gulls, Terns

Family Rynchopidae, Skimmers

Suborder Alcae

Family Alcidae, Auks, Auklets, Murres

Wetmore, 1960

INTRODUCTION

With over 300 species the Charadriiformes is one of the largest of avian orders, exceeded only by the Psittaciformes, Apodiformes, Piciformes, and Passeriformes. Adaptive radiation in the order has produced limicoline (plovers and sandpipers),

aerial-littoral (gulls), and natatorial (alcids) forms. These assemblages together with several satellite groups constitute the Charadriiformes of Peters (1934) and Wetmore (1960). The precise relationships of the satellites to the main groups are not obvious. In this regard the following questions arise:

1) Are the jacanas or lily-trotters (Jacanidae) most closely allied to the painted snipe (Rostratulidae) and other charadriiform groups, or are they actually related to the rails, to which they show some similarities?

2) Are the Alcidae charadriiforms, or are their superficial similarities to the diving petrels (Pelecanoididae) and penguins (Spheniscidae) indicative of a close relationship to either or both of these groups?

3) Do the seedsnipe (Thinocoridae) belong to the Charadriiformes or are they allied instead to the Galliformes, the Turnicidae, or the Pteroclididae, all of which share some similar adaptations?

4) Is the family Glareolidae (pratincoles and coursers) a monophyletic group? Did they descend from the larine or pluvialine branch in charadriiform evolution?

5) To which groups are the crab-plover (*Dromas*) and sheathbills (*Chionis*) most closely related?

6) Are the skimmers (*Rynchops*) highly modified gulls, or terns?

7) Are the thick-knees (Burhinidae) more closely related to the plovers or to the bustards?

8) To what degrees are the Charadriiformes related to the Gruiformes, *Pterocles*, the Columbidae, the Gaviiformes, and the Procellariiformes?

HISTORICAL REVIEW OF THE CLASSIFICATION

In most of the classifications proposed before 1867 the gulls were placed near the shearwaters or the tropic-birds, the auks were associated with the penguins, and the plovers and sandpipers were allied with the herons, rails or bustards. Even Nitzsch (1840), whose pterylographic evidence provided valid clues in several similar cases, placed *Alca* with *Spheniscus*, the Laridae beside the Procellariidae and the scolopacids in a different major subdivision from the other charadriiforms. However, Nitzsch did note that the pterylosis of the Laridae is extremely similar to that of the Scolopacidae.

The recognition of the relationships among the presently accepted subgroups of the Charadriiformes began to take more definite shape in 1867 when Huxley placed the schizognathous birds together. His suborder Schizognathae contained nine "Groups", two of which included the charadriiforms. Group 1, the Charadriomorphae, was composed of the Charadriidae and Scolopacidae. Group 2 (Geranomorphae) included the Gruidae, plus *Psophia* and *Rhynochetos*, and the Rallidae, plus *Otis* and *Cariama*. Group 3, the Cecomorphae, contained the Laridae, Procellariidae, Colymbidae (= Gaviidae) and Alcidae. The penguins were placed in another group, the Spheniscophorphae. Thus, the auks and gulls were together for the first time and the auks were separated from the penguins. However, during the same period Coues (1868) placed the Spheniscidae, Alcidae, Gaviidae and Podicipedidae together in his order Pygopodes. Coues (p. 10) was dogmatic about his belief that "the position occupied by the Auks in this order is so evident as not to admit of question."

Garrod (1873d, 1874a) included nearly all of the schizorhinal birds in his Charadriiformes. He recognized two cohorts, the Columbae (including *Pterocles*) and the Limicolae. He divided the Limicolae into four families, the Charadriidae

(including *Glareola*, *Haematopus*, *Himantopus*, and *Actophilornis*), Gruidae, Laridae, and Alcidae. *Burhinus* was placed with the bustards in a separate order, Galliformes, which included the ratites, gallinaceous birds, rails and cuckoos. Garrod (1877a) also made an anatomical study of the Thinocoridae. He confirmed that their pterylosis is most like that of the shorebirds and pointed out several differences between the seedsnipe and the Turnicidae. In his opinion, the closest allies of the thinocorids are *Cursorius* and *Glareola*. As evidence for this relationship he cited the absence of an articulation of the pterygoid to the basisphenoidal rostrum, the absence of supra-occipital foramina, and similarities in palatal structure and myology. Garrod also drew attention to the extensive variation in the shape of the vomer in the charadriiforms. Most members of the group have a "schizognathous" palate in which the vomer is pointed anteriorly but in the Thinocoridae the vomer is broad anteriorly and therefore "aegithognathous."

P. Sclater (1880), who mainly followed Huxley's scheme, came very close to the arrangement of Wetmore (1960) except for his placement of the Alcidae with the loons and grebes in the "Pygopodes." However, the other charadriiforms were placed in adjacent orders; the Laridae in the Gaviae and the remaining groups, including the thick-knees, in the Limicolae. The bustards were allied with the other gruiforms and the penguins were separated in the order Impennes.

The controversy over the position of the jacanas was reviewed by Forbes (1881a) and new anatomical evidence was presented. The "Parridae [= Jacanidae] form a well-marked family" in his Pluviales, with their closest relatives possibly being the Charadriidae, "from which they are easily distinguishable by the absence of supra-orbital glands and occipital foramina, by their enormously elongated toes, by the number of rectrices, and other points" (p. 647).

The following characters are shared by the Chionididae and Thinocoridae (Stejneger, 1885): 1) schizorhinal nares; 2) supraorbital impressions; 3) pelvic muscle formula of Garrod ABXY+; 4) two carotids; 5) vomer broad and rounded in front; 6) absence of occipital foramina and basiptyergoid processes. Stejneger also observed (p. 92) that in the palate of the thinocorids the vomer is connected with the nasal cartilages "in a manner recalling that of the Aegithognathae." An aegithognathous palate, or a tendency toward it, is also found in *Turnix*, the swifts, *Indicator*, some barbets and the Passeriformes. Stejneger placed the auks and gulls together but allied them with the loons, sungrebes and procellariiforms in the order "Cecomorphae." The other charadriiforms were placed with the gruiforms in the order "Grallae."

Seebohm (1888a) wrote an extensive monograph on the Charadriidae, which was one of eight families comprising his suborder Limicolae of the Charadriiformes. Regarding the nearest allies of the Limicolae, he wrote (p. 5): "The Pteroclididae form a stepping stone to the Pigeons, the Turnicidae and Thinocoridae to the Game Birds, the Dromadidae to both the Gulls and the more distant Herons, whilst the Chionidae form a second link to the gulls, the Parridae to the Rails, and the Otididae to the Cranes." Seebohm's Charadriidae included the plovers and sandpipers as well as the Burhinidae, Glareolidae, and Recurvirostridae. Seebohm (1888b), "by the aid of osteological characters alone," diagnosed a series of suborders "of the great Gallinigralline Group of Birds." In his "Gavio-Limicolae" Seebohm included the Laridae, *Dromas*, *Chionis*, Thinocoridae, Alcidae, Charadriidae, Scolopacidae, Glareolidae and Burhinidae. Thus, the group included most or all (Jacanidae not mentioned) of Wetmore's (1960) Charadriiformes. (Note: the terms Gavio, Gaviae, etc., of this period refer to the gulls and their allies, not to the loons or divers [*Gavia*], which were at that time placed in the genus *Colymbus*.)

Seebohm (1890a) recognized the suborders Gaviae (gulls and auks) and

Limicolae for the charadriiform birds. These two suborders formed part of his order Gallo-Grallae, a large assemblage also containing the gruiform, galliform, gaviiform, podicipediform, and tinamiform birds. The Charadriiformes of Seebohm (1895) included the suborders Gaviae, Limicolae, Grues, Pterocles, and Columbae. Within the Limicolae he recognized the families Charadriidae and Parridae (= Jacanidae). The Thinocoridae, Chionididae, and Glareolidae were lumped into his family Cursoriidae of the suborder Gaviae.

The osteology of the surfbird (*Aphriza virgata*) was studied by Shufeldt (1888d), who concluded that it is more closely related to the sandpipers than to the plovers. He erected monotypic families for *Aphriza* and *Arenaria*.

Fürbringer (1888) included in his "suborder" Charadriiformes the Charadriidae, Glareolidae, Dromadidae, Chionididae, Laridae, Alcidae, Thinocoridae, Parridae [= Jacanidae], Oedicnemidae [= Burhinidae] and Otididae. Except for the inclusion of the bustards (Otididae) these groups contain the same species as in Wetmore's (1960) Charadriiformes, thus indicating again the antecedent importance of Fürbringer's classification to those currently in use. Fürbringer placed the painted snipe (*Rostratula*) in a separate subfamily and noted similarities to the jacanas as well as to the scolopacines.

In his study of intestinal convolutions Gadow (1889) found resemblances among the plovers and sandpipers ("Limicolae"), the Laridae and the Columbidae. The Rallidae and Alcidae were similar to these groups but also showed differences.

Shufeldt (1891c) published a study of the osteology of *Chionis* and reviewed (1893a) the opinions on the systematic position of the sheathbills (Chionididae). He proposed (p. 165) a suborder Chionides to "stand between my suborder Longipennes [= Procellariiformes] and the suborder Limicolae." He thought that the Dromadidae and Thinocoridae might be included in his Chionides.

Sharpe (1891) presented a critical and extensive review of "recent attempts to classify birds" and offered his own classification accompanied by a descriptive commentary. The charadriiforms were arranged in three orders: the Alciformes (Alcidae), Lariformes (Stercorariidae, Laridae) and Charadriiformes (Dromadidae, Chionididae, Attagidae, Thinocoridae, Haematopodidae, Charadriidae, Scolopacidae, Glareolidae, Cursoriidae, Parridae, Oedicnemidae and Otididae). He did not "agree with placing the Auks with the Lari" and, although admitting that the two groups are related, considered the Alcidae to be "the nearest . . . to the outlying Tubinares" (p. 61). He admitted "the close affinity of the Charadrii and Lari" (p. 62) and noted that the jacanas combine charadriine and ralline characters. The bustards (Otididae) were included in his Charadriiformes because of their resemblance to the thick-knees (Oedicnemidae = Burhinidae).

A new classification based upon "about forty characters from various organic systems" was proposed by Gadow (1892: 230). Of these 40 characters he found that the "Lari agree with Alcae and with Limicolae in 33 or 34; Limicolae agree with Alcae, Lari, and Ralli each in 33, with Pterocles and Columbae in 30 or 31, with Gallidae in 26." Gadow's Charadriiformes based upon these analyses includes the same groups as in Wetmore's (1960) order Charadriiformes. Gadow placed the bustards in his Gruiformes and thus separated the Otididae from the Burhinidae.

Wetmore (1930: 1) based his classification upon that of Gadow (1893) and, thus, if we are to question any aspects of the "modern" classification we must return to that of Gadow. The latter included the pigeons and sandgrouse in the Charadriiformes, thus indicating his conviction that these are related groups.

The Laridae of Beddard (1896a) included the subfamilies Sterninae, Rynchoptinae, Larinae, and Stercorariinae. *Rynchops* differs from the other Laridae in its

pelvic muscle formula and in lacking the biceps slip. It agrees with the Larinae and Sterninae in possessing small caeca, and, like the Sterninae and Stercorariinae, has the expansor secundariorum.

Beddard (1898a) made two orders, Limicolae and Alcae, for the charadriiforms. He also accorded an order, Otides, to the bustards and commented upon their similarities to both gruiforms and charadriiforms, especially to the thick-knees (Burhinidae). Beddard (1901c) also studied the painted snipe (Rostratulidae of Wetmore, 1960) and compared their anatomy with that of *Gallinago*, *Scolopax*, and other charadriiforms. He concluded that the painted snipe are not closely related to the Scolopacidae and agreed "to some extent with Dr. Fürbringer's opinion that an alliance with the Parridae [= Jacanidae] is not at all unreasonable" (p. 587).

A similar pattern of intestinal coiling in the charadriiforms and gruiforms, including the Turnicidae, was found by Mitchell (1896a, 1901a). Other groups in his "Alectoromorphine Legion" were the Tinamidae, Columbidae, Pteroclididae, *Opisthocomus*, and Galliformes. Beddard (1910) severely criticized Mitchell's conclusions based upon the intestinal tract and, from his own studies, presented strongly opposing views. Beddard's remarks concerning the Charadriiformes include the following:

1) "Among the Limicolae, with which . . . the Gulls and Terns are . . . to be placed, there are several variations . . ." (p. 74).

2) The Alcidae are unlike the gulls and should be treated as "a distinct assemblage or . . . associated with the Grebes and Divers . . ." (p. 78).

3) The condition in the alcid *Fratercula* was also considered to be similar to that in an "abnormal" specimen of the pheasant "*Euplocamus nycthemerus*" (= *Lophura nycthemera*).

4) The "Ralli are a . . . circumscribed group . . . which bear only a general resemblance to other groups and . . . to no group in particular" (p. 90).

5) It "is by no means possible to distinguish . . . the intestinal tract of a Grebe or Tern from that of the Owls . . . or large Passerine birds . . . ; while the Gulls and Terns . . . offer resemblances to . . . 'the other' Limicoline birds" (p. 90).

The disagreements between Beddard and Mitchell discredit the taxonomic value of the intestinal coiling patterns and demonstrate again the difficulties involved in the interpretation of morphological characters.

Shufeldt (1903a) produced an extensive dissertation on the osteology of the shorebirds and proposed a "supersuborder" Lariformes for the skimmers, jaegers, gulls, terns, auks and sheathbills and a "supersuborder" Charadriiformes for the remainder of Wetmore's (1960) Charadriiformes. Shufeldt included the bustards with the thick-knees in a superfamily, Otidoidea, and agreed with Forbes (1881a) that the jacanas are charadriiform, not gruiform. This same classification was included in Shufeldt's (1904b) arrangement of families and higher groups.

Studies of the myology and wing pterylosis in the limicoline charadriiforms were published by Mitchell (1905) and he repeated some of his earlier observations on the intestinal coiling patterns. His suborder Limicolae included the Charadriidae (including the Scolopacinae), Chionidae, Glareolidae, Thinocoridae, Oedicnemidae [= Burhinidae], and Parridae [= Jacanidae]. His summary (p. 169) stated: "With the exception of *Oedicnemus*, the Limicoline birds examined, so far as relates to the characters dealt with, show a definite and coherent series of modifications. The group is moving, or has moved, along the same anatomical lines. The limits of its variations overlap in a special way the variations displayed by Gulls, and in a general way those exhibited by Gruiform birds." We interpret this to mean that Mitchell saw evidence of close relationships between the Limicolae and the gulls and a somewhat more distant alliance to the gruiforms.

In the opinion of Chandler (1916: 358), the "unquestionable likeness of the structure of feathers in the Alcidae to that in the Colymbiformes [loons and grebes] very strongly suggests the close relationship between them. The relation of the Laridae to the Alcidae, and of the Limicolae to the Laridae, is just as plainly indicated. . . . Relationship to the Gruidae is also suggested and it is probable that the latter represent an early offshoot from the limicoline stem." Chandler, however, thought that the feather structure of *Cursorius* indicated a close relationship to the Ardeidae.

Mathews and Iredale (1921) were impressed by the general similarity of the Thinocoridae to the gallinaceous birds and placed them in their order Galli. Without explanation they stated: "The internal characters cited in favour of a Charadriiform alliance were obviously misunderstood" (p. 217).

In 1914 Lowe began publishing what was to be an extensive series of papers on the relationships of the charadriiform birds. He observed that the color patterns among adult plovers of the genus *Charadrius* were more similar than, for example, the sizes and shapes of the bills. He also discovered that the downy young of *Charadrius* have a uniform color pattern and reasoned that this character would be of value in assessing relationships at the generic level. From the simple nature of the color pattern and the cosmopolitan distribution of *Charadrius* Lowe postulated that all other plovers were derived from the ring-plover group. In a subsequent paper (1915a) he furnished additional examples in support of this idea. Among the sandpipers he could distinguish the subfamilies Erolinae and Tringinae on the basis of the color pattern of the downy young. In his opinion, the ruff (*Philomachus pugnax*) and snipe (*Gallinago*) are eroliine, but the phalaropes (*Phalaropus*) are tringine. Lowe believed that the mutations producing a certain type of color pattern are selectively neutral, and he doubted that variations in the intensity of pigmentation have a genetic basis. We now understand that the breast bands and head markings in *Charadrius* have selective value in that they create a disruptive pattern which tends to conceal a bird sitting on a nest. The variations in these features among species of *Charadrius* suggest that they may function also as species-specific signal characters.

Lowe (1915b) presented osteological evidence that agreed with his interpretation of the plumage patterns of the downy young. He was able to separate the Erolinae and Tringinae on the basis of several characters of the palate, the premaxilla, the lachrymals, the angle formed by a line along the culmen of the bill and another along the basisphenoidal rostrum, and other aspects of the skull. In these characters *Philomachus*, as well as *Ereunetes* and *Micropalama*, agree with the Erolinae, not the Tringinae.

The osteology of the snipe-like New Zealand genus *Coenocorypha* resembles a woodcock (*Scolopax*) more than it does a snipe (*Gallinago*), according to Lowe (1915c). He regarded *Coenocorypha* as a relict form once having a wider distribution and which may have been part of a group ancestral to the Scolopacinae.

Lowe next focused his attention on the relationships of the Chionididae. He (1916a,b) examined the pterylosis of both species of *Chionis* and the osteology, mainly cranial, of both adults and embryos. He found little to suggest an alliance between the sheathbills and either the gallinaceous or columbiform birds. He compared *Chionis* to a variety of shorebirds and decided that it shared more characters with plover-like forms, especially *Haematopus*, than with gull-like forms such as *Stercorarius*. He believed that the sheathbills are specialized charadriiforms and expressed the following opinion regarding their probable evolution (1916a: 152):

It is probably nearer the truth to suppose that the Sheath-bills were differentiated as an offshoot from the main charadriiform stem before that stem had split into the charadriine and scolopacine branches, and that that offshoot was given off

prior to the differentiation of the Skuas and Gulls; or, as an alternative speculation, that the main charadriiform stem split into a limicoline and a larolimicoline branch—such groups as the Sheath-bills, Crab-Plover, Pratincoles, Skuas, Gulls, Terns, and Auks arising from the latter by various stages of specialization.

An investigation of the pterylosis and osteology of the crab-plover (*Dromas ardeola*) by Lowe (1916b) did not clarify the relationships of *Dromas*, and he was able to suggest only that, like a gull, it is probably a "specialized plover." He felt that *Dromas* was best kept in a separate group within the Charadriiformes.

Lowe (1922) returned to a consideration of color and color patterns in plovers. He suggested that light dorsal coloration, as in the Kentish plover (*Charadrius alexandrinus*), is a primitive condition. He also found that the plovers varied in the development of supraorbital furrows for the nasal gland and argued that this character is correlated with the color of the back. Thus, in Lowe's opinion, an "advanced" charadriid would be one with a dark back and relatively high degree of ossification in the supraorbital ridges. He divided the plovers into four subfamilies on these bases and on other characters of the skull. At that time he presented a provisional classification of the Charadriiformes in which he recognized three suborders. The suborder Limicolae contained the Scolopacidae (including the phalaropes) and Charadriidae (including *Haematopus*, the jacanas, and the painted snipe). The Lari-Limicolae included the Glareolidae, Dromadidae, and Chionidae as well as the gulls and auks. The Burhinidae were the sole members of the suborder Oti-Limicolae. Lowe was uncertain of their relationships to the bustards. He excluded the Thinocoridae from his Charadriiformes.

Lowe (1923) thought that the seed-snipie may represent a basal group of the Charadriiformes or "that they, together with the families Turnicidae and Pteroclididae, should be regarded as the still-surviving blind-alley offshoots or relics of an ancient generalised and basal group (now extinct), from which group sprang the Schizomorphs or the now dominant Pigeons, Plovers, and Fowls" (p. 277).

Lowe (1925b) presented evidence from pterylosis and pelvic structure in favor of an alliance of the Jacanidae to the Rallidae, and not to the Charadriidae as he had proposed in 1922. Lowe also discovered that the Charadriiformes differ from the Gruiformes in the morphology of the quadrate-tympanic articulation. In this character the Jacanidae are gruiform, according to Lowe. The apparent value of this character led to an examination of other groups (Lowe, 1926). When he inspected the quadrates of *Thinocorus* and *Attagis*, he modified his previous opinion (1923) of their relationships and proclaimed the seed-snipie to be "undoubtedly" charadriiform. Similarly, he concluded that the morphology of the quadrate of *Chionis* "is absolutely typical of the pluvialine as opposed to the larine division of the Charadriiformes" (1926: 185). He also suggested that the surfbird (*Aphriza*) and the willet (*Catoptrophorus*) are closely related to the sandpipers and not to the plovers as he had earlier believed (1922: 492; 1925b: 147).

An extensive study of the anatomy of the scolopacid *Aechmorhynchus cancellatus* led Lowe (1927) to conclude that this species is a "generalised Scolopacine type . . . in which a tendency to specialize in the direction of the Curlew group had early occurred" (p. 116).

In 1931 Lowe published two lengthy papers as the culmination of his work on the Charadriiformes. In the first of these (1931a) he presented data from anatomy, pterylosis and downy plumage patterns. His principal conclusions were:

- 1) The painted snipe should be referred to a family, Rostratulidae, in the Limicolae.

2) The rails should be removed from the Gruiformes and treated as a separate order, the Ralliformes, which includes the Rallidae and Heliornithidae.

3) The gruiforms (Gruidae, Psophiidae, Aramididae, Rhynochetidae, Eurypygidiae, Otididae, Burhinidae, Jacanidae and, perhaps, the Cariamidae) should be combined with the charadriiforms as a suborder Grues in the order Telmatomorphae.

4) The Telmatomorphae also includes the suborders Limicolae (Rostratulidae, Charadriidae, Scolopacidae) and Laro-Limicolae (Thinocoridae, Glareolidae, Chionidae, Dromadidae, Laridae).

Lowe's concluding remarks (p. 532) summarize the above proposals and note that "one of the most striking facts that has emerged from my anatomical studies is the decidedly gruine character of the Burhinidae, so that one has . . . been led to wonder why they have so persistently been referred to the Limicolae—and this also applies to the Jacanidae; while . . . the Rostratulidae . . . represent an ancient group with leanings towards the Gruae, yet . . . more limicoline than gruine."

In his next paper (1931b) Lowe made some further changes, as follows: the Thinocoridae were removed from the Lari-Limicolae and placed in a special suborder, Grui-Limicolae; the skuas, gulls and auks were removed from the Lari-Limicolae to a new suborder, Lari. Lowe's "final classification of the telmatomorphine suborders" was therefore as follows:

Grues: as listed above (#3).

Grui-Limicolae: Thinocoridae.

Limicolae: Rostratulidae, Charadriidae, Scolopacidae.

Lari-Limicolae: Glareolidae, Dromadidae, Chionidae.

Lari: Stercorariidae, Laridae, Alcidae.

Lowe provided extensive anatomical data to support his conclusions and included discussions of the Thinocoridae, various limicoline genera, *Rostratula*, the sheathbills, crab-plovers, Glareolidae, and others.

Lowe's last paper on the shorebirds (1933b) primarily concerned correlations between plumage color and color pattern and the development of the supraorbital (or nasal) glands in the plovers. He noted that there tend to be pairs of species in which one has a pale, "adumbrated" plumage and deep supraorbital grooves and the other species has more intense plumage colors and color pattern correlated with shallow supraorbital grooves. Lowe was aware of the correlation between the size of the supraorbital gland and a salt versus fresh water habitat but felt that this did not completely explain the situations he had found. However, W. Bock (1958) criticized Lowe's interpretations and concluded that the size of the supraorbital glands is of no taxonomic value (see below).

Dwight (1925) published a detailed study on the molts and plumages of gulls. His classification was based entirely on external characters and required nine genera for 44 species of gulls.

E. Stresemann (1927-34) required four orders for the charadriiform birds. He placed the Alcae next to the Laro-Limicolae and considered the Alcidae to be most closely allied to the Laridae. He believed that the Jacanae (Jacanidae) were related to the Ralli (Rallidae) and to the Laro-Limicolae. In his opinion, the Thinocori (Thinocoridae) are allied to the Grues (Gruidae, Aramididae) and to the Laro-Limicolae, but more closely to the latter. Stresemann also mentioned that the Otides (Otididae) may be distantly related to the Laro-Limicolae.

The literature of the Charadriiformes from 1894 to 1928 was reviewed by Low (1931). His classification of the order included the suborders Oti-Limicolae (Otididae, Burhinidae), Limicolae (plovers, sandpipers, others), and Lari-Limicolae (*Dromas*, *Chionis*, Glareolidae, Thinocoridae).

Von Boetticher (1934) classified the Charadriiformes into the suborders Ptero-

clites, Burhini (Otididae, Burhinidae, Dromadidae), Thinocori (Thinocoridae, Chionidae), and Laro-Limicolae (Glareolidae, Cursoriidae, Laridae, Alcidae, Charadriidae).

Hudson (1937) studied the pelvic muscles in one or more species representing 16 of the 20 orders of birds of North America, including two scolopacids (*Totanus*), a larid (*Larus*), and an alcid (*Uria*). He found a rudimentary ambiens muscle in *Uria* although the alcids "are generally stated to lack this muscle." Hudson noted (p. 77) that Gadow (1891) had recorded the ambiens in *Uria* "but this apparently has escaped the notice of taxonomists." Using his "amplified" formula Hudson determined the pelvic muscle formulas of the genera he dissected to be: *Totanus*, ADXY Am V; *Larus*, ACDXY Am V; *Uria*, ABDX Am. He also provided information on the deep flexor tendons and other modifications of the myology of the pelvic appendage.

A. Miller and Sibley (1941) described *Gaviota niobrara* from the upper Miocene of Nebraska on the basis of the distal quarter of a humerus. This fossil, although clearly that of a gull, showed some similarities to the Scolopacidae (e.g., *Numenius*) and led the writers to suggest that the two groups may have been more closely related in Miocene times.

The structural modifications in the hind limb of the Alcidae were studied by Storer (1945a). He noted (p. 452) that his proposed arrangement of the genera agreed best with that of Dawson (1920), which was based upon eggshell characters. Storer proposed "seven groups of suprageneric rank" for 14 genera and (1945b) reviewed the systematic position of the genus *Endomychura*, concluding that it is closer to *Synthliboramphus* than to *Brachyramphus*. Storer (1952) also studied variation in external morphology and behavior in *Cepphus* and *Uria* and concluded that, unlike the Alcidae as a whole, *Uria* probably originated in the Atlantic region. He suggested that *Cepphus* is closer to the ancestral alcid stock than is *Uria*.

Several aspects of the fossil record of the Charadriiformes were reviewed by Howard (1950). She expressed the opinion that the shorebirds and Gruiformes may have had a common ancestry, noting that the genus *Rhynchaetes* from the middle Eocene of Germany combines characters of both shorebirds and rails. Howard pointed out that the allocation of many fossil charadriiforms is open to question since most of the extant families are not readily distinguishable on the basis of unassociated skeletal elements.

Concerning the shorebirds Mayr and Amadon (1951) wrote: "This diversified order may be connected with the Grues through one or all of the Burhinidae, Jacanidae, and Thinocoridae. Several of the shore bird families currently recognized seem to require no more than subfamily status. . . ." Their arrangement is that of Wetmore with the Scolopacidae, Phalaropodidae, Recurvirostridae, and Rostratulidae reduced to subfamily rank within the Charadriidae, and the Stercorariinae, Sterninae, and Rynchopinae as subfamilies of the Laridae.

Von Boetticher (1954) criticized the large number of genera into which Peters (1934) had arranged the lapwing plovers and proposed that the 25 species be placed in four genera, rather than the 19 of Peters.

The structure of the esophagus of *Thinocorus orbignyianus* was compared with that of *Pterocles* and several shorebirds by Hanke and Niethammer (1955). Their data agreed with the inclusion of the seedsnipe in the Charadriiformes.

Differentiation among the Palearctic Charadrii during the Tertiary period, particularly in the Pleistocene, was analyzed by Larson (1955, 1957). While his detailed conclusions regarding evolution and speciation are outside the scope of this paper, his work will be of interest to those studying species relationships among the plovers and sandpipers.

Verheyen (1957d) proposed an order, Jacaniformes, to contain the Eurypygidae, Rhynchetidae and Jacanidae. He believed that these families were as close to the "Ralliformes" as to the Charadriiformes and should therefore be placed between them. A new classification of the Charadriiformes based upon anatomical characters was proposed by Verheyen (1958d). His Charadriiformes included the families Chionidae, Haematopidae, Charadriidae, Scolopacidae, Tringidae, Rostratulidae, Glareolidae, Dromadidae and Burhinidae. Verheyen considered this group to be related on one hand to the "Columbiformes and the Turniciformes and on the other to the Lariformes, the Jacaniformes and the Ralliformes" (p. 31; our translation).

Verheyen (1958b) proposed that an order, Alciformes, be recognized to include the diving petrels, Pelecanoididae, and the Alcidae. This group, he suggested, is allied to the "Lariformes, aux Procellariiformes et aux Sphenisciformes." He believed that the "Lariformes and the Procellariiformes on one side, the Sphenisciformes and the Alciformes on the other, have not acquired a similar appearance due to the phenomenon of convergence but rather from the effects of a paramorphogenic evolution" (p. 14; our translation). Verheyen retained the gulls and their allies as a separate order next to the Charadriiformes. His arrangement was:

Order Lariformes

Suborder Rynchopi: Rynchopidae

Suborder Lari: Laridae (subfamilies Larinae, Sterninae, Gyginae: *Gygis*)

Stercorariidae (subfamilies Stercorariinae, Anoinae: *Anous*).

Timmerman (1957a,b) used the evidence from the Mallophaga to suggest relationships among the Charadriiformes. Among his main conclusions are the following:

- 1) The gulls and the shorebirds are more closely related to each other than either is to the auks, so that two suborders rather than three best represent the relationships.
- 2) *Rynchops* is most closely related to the terns.
- 3) *Arenaria* belongs in the Scolopacidae, not the Charadriidae.
- 4) *Limnodromus* and *Limosa* are closely related to each other and belong in the subfamily Erolinae (= Calidridinae), not in the Scolopacinae or Tringinae.

In subsequent papers (1959, 1962, 1965) Timmerman developed and defended the proposal that the nearest allies of the Charadriiformes are the Procellariiformes.

A generic review of the plovers (Charadriinae) led W. Bock (1958) to review past classifications and to carry out an extensive study of the skull. He found that the condition of the hind toe, the wattles and the wing spur were of little or no taxonomic value, and that color and color pattern must be used with caution. He was unable to find characters in the body skeleton which were "useful in understanding relationships within the plovers" (p. 54). He showed that the "degree of ossification of the supraorbital rims is strongly correlated with the size of the nasal glands and hence with the salinity of the water, and is of no taxonomic value" (p. 90). Lowe's interpretations of skull morphology and color pattern were criticized as being "at variance with many of the observed facts and with many of the ideas and principles of evolution and classification" (p. 90). Bock proposed a new classification of the plovers in which the subfamily Charadriinae also includes the Vanellinae of Peters (1934). The 61 species and 32 genera recognized by Peters were reduced to 56 species placed in 6 genera. *Arenaria* and *Aphriza* were considered to be scolopacids.

Bock (1964) studied the rather aberrant Australian dotterel (*Peltohyas australis*) and concluded that it is charadriine, not glareoline. This conclusion was later disputed by Jehl (1968a), who placed *Peltohyas* in the Cursoriinae.

Storer (1960b) reviewed the evidence on the evolutionary history of the diving birds and reaffirmed his belief in the existence of two major phylogenetic lines containing convergently similar species, namely, a penguin-procellariiform group and a

shorebird-gull-auk (charadriiform) group. The loons (Gaviiformes) were possibly derived from the common ancestor of the charadriiform lineage, with the fossil *Colymboides* a possible link.

Several studies on the behavior of gulls were published by Moynihan (1955; 1956; 1958a,b; 1959a; 1962). His revision of the Laridae (1959b) is based on his observations and those of others, especially Tinbergen (1959). Moynihan's classification is summarized as follows:

Subfamily Stercorariinae

Stercorarius (including *Catharacta*).

Subfamily Larinae

Tribe Larini: *Larus* (including *Gabianus*, *Pagophila*, *Rhodostethia*, *Rissa*, *Creggrus*, *Xema*)

Tribe Rynchopini: *Rynchops*

Tribe Sternini: *Anous* (including *Procelsterna*, *Gygis*), *Larosterna*, *Sterna* (including *Chlidonias*, *Phaetusa*, *Gelochelidon*, *Hydroprogne*, *Thalasseus*).

Wetmore (1960) divided the Charadriiformes into three suborders: the Alcae (auks, murre, puffins), Lari (gulls, terns, jaegers, skimmers), and Charadrii (the remaining groups). He disputed Moynihan's lumping of *Rynchops* in the Laridae and felt that the skimmers deserve family rank. Wetmore wrote (p. 13):

The bill, compressed to knifelike form, with great elongation of the ramphotheca [*sic*] of the lower jaw, is unique, and the method of feeding, where the lower mandible cuts the water surface with the bird in flight, is equally strange. The structural modifications in the form of the skull from that found in skuas, gulls, and terns also are too extensive to be ignored. The elongated blade of the lower mandible anterior to the symphysis of the rami is intriguing but less important than the profound changes found elsewhere. The palatine bones are greatly expanded, the orbital process of the quadrate is reduced to a short, pointed spine, the impression for the nasal gland is much reduced, the frontal area is inflated and produced posteriorly, with compression of the lachrymal, and consequent reduction in size of the cavity for the eye, to enumerate the most outstanding differences in the osteology. Externally, the pupil of the eye is a vertical slit similar to that of a cat, and thus unlike that of any other group of birds. . . .

The feeding adaptations in the head and neck region of the black skimmer (*Rynchops nigra*) were studied by Zusi (1962). Although he enumerated some similarities to the terns, Zusi did not draw taxonomic conclusions from his data. Instead he concluded (p. 96): "The skimmers seem to embody a mixture of gull-like and tern-like characteristics, on which is superimposed a highly developed adaptive complex associated with feeding. This complex involves anatomy and behavior. It is probable that many morphological features of the entire body have been altered during the evolution of the unique feeding method, and that many of the behavior patterns, other than skimming, have been secondarily affected."

Sibley (1960) compared the paper electrophoretic patterns of the egg white of 11 of the 16 charadriiform families recognized by Wetmore (1960). He found a "readily detectable common pattern" in the order although there was much minor variation among the patterns. The egg white pattern of *Rostratula* was quite different from those of the other shorebirds and Sibley felt that the painted snipe are best retained as a separate family. Among other groups the patterns of the Gaviidae and some Rallidae were most similar to those of the Charadriiformes.

E. Stresemann (1959) emphasized the lack of convincing evidence for the affinities of several shorebird groups by recognizing the same four orders that he had in 1934. Subsequently E. and V. Stresemann (1966: 212) found that the molt of primaries in the Thinocoridae begins in an ascending fashion with primary 10, but after the eighth or seventh primary is lost, the replacement proceeds irregularly. Although this pattern differs from that of other shorebirds, in which the primary molt is regularly ascending, other aspects of molt, the form of the wing, and the number of secondaries and rectrices are the same, the Stresemanns (p. 222) held the opinion that the Thinocoridae seem to be closely allied to the Charadriidae and Scolopacidae.

In his final classification of the non-passerines Verheyen (1961) presented an arrangement that once again demonstrates the inability of his methods to distinguish between similarities due to convergence and those reflecting common ancestry. A synopsis of the portion including the shorebirds follows.

Superorder Hygrornithes

Order Sphenisciformes: Spheniscidae

Order Procellariiformes: Procellariidae, Diomedeidae, Hydrobatidae

Order Alciformes: Pelecanoididae, Alcidae, Gaviidae

Superorder Limnornithes

Order Pelecaniformes: Anhingidae, Phalacrocoracidae, Sulidae, Pelecanidae

Order Lariformes: Fregatidae, Phaethontidae, Rynchopidae, Laridae, Stercorariidae

Order Charadriiformes: Chionidae, Charadriidae, Calidridae, Scolopacidae, Glareolidae, Dromadidae, Burhinidae, Rostratulidae

Order Jacaniformes: Mesitornithidae, Rhynochetidae, Eurypygidae, Jacanidae

McFarlane (1963) examined the sperm morphology of a number of avian groups by phase-contrast microscopy. He found that members of the Charadriidae, Recurvirostridae, Laridae, and Alcidae have sperm of similar structure, but that members of the Scolopacidae differ, having sperm of an elongate spiral shape. The only other order in which McFarlane observed spiral-shaped sperm was the Passeriformes. He (1963) reasoned that spiralization may be a recent evolutionary trend and suggested that the Scolopacidae may have had a more recent origin than the other Charadriiformes.

Erythropoiesis in the yolk sac, liver, spleen, and bone marrow from the tenth embryonic day to the first postembryonic day was studied in a number of avian groups by Schmekel (1962, 1963). *Vanellus*, *Larus*, and *Uria* showed erythropoiesis in the yolk sac up to the twentieth embryonic day or longer. The onset of hematopoiesis in the bone marrow did not depend on the date of hatching and immediately superseded erythropoiesis in the yolk sac. A short transient period of erythropoiesis in the liver was also observed. That the three species are similar to one another in these characters and differ from all others examined indicated to Schmekel a close relationship among the shorebirds, gulls, and auks.

Using paper electrophoresis Perkins (1964) examined the hemoglobins and serum proteins of seven species of gulls (*Larus glaucescens*, *argentatus*, *canus*, *occidentalis*, *californicus*, *delawarensis*, and *philadelphia*). The hemoglobin patterns of all species were identical and showed two components. Some fractions in the serum pattern varied within a species, and the author was unable to separate the different species on this basis.

Gysels (1964a) and Gysels and Rabaey (1964) examined the lenticular and muscle proteins of *Alca torda*, *Uria aalge*, and *Fratercula arctica* by zone electro-

phoresis and immunoelectrophoresis in agar gel. They believed that their electrophoretic evidence, as well as the absence of glycogen in the lens, indicated a close relationship between *Uria* and the penguins. They also concluded that *Alca* and *Fratercula* differ from the Charadriiformes, from *Uria*, and from each other. Sibley and Brush (1967) have cast doubt on the value of electrophoretic comparisons of the lenticular proteins in higher category systematics and we present here some additional points. The published figures in Gysels and Rabaey (1964) are difficult to evaluate because the origins are not properly aligned, and the diffuse nature of the main bands in their patterns of *Uria*, *Alca*, and *Fratercula* may indicate that some denaturation of the proteins has occurred. Gysels and Rabaey tested the lenticular proteins of the species in their study for reactivity with antisera prepared against the lenses of the chicken and starling (*Sturnus vulgaris*). We believe that immunological comparisons among such widely separated groups cannot be wholly satisfactory. To eliminate as far as possible the problem of spurious cross-reactions, antisera to all of the species involved should be prepared and the reciprocal tests for cross-reactivity should be made. Finally, the Alcidae on nearly all grounds are a closely knit group of birds. To suggest their fragmentation into two or three diverse groups without a thorough reconsideration of their morphology and without extensive biochemical comparisons seems unwise.

Holmes and Pitelka (1964) compared various behavioral characters of the curlew sandpiper (*Calidris ferruginea*) and concluded that it seems to bridge the gap between the pectoral sandpiper (*C. melanotos*) and the more typical species of the genus, sometimes placed in *Erolia*.

From an immunological study of the serum proteins of the Alcidae, Averkina, Andreyeva, and Kartashev (1965) concluded that *Uria* and *Cepphus* are most closely related. *Alca* is next closest to them, and *Fratercula* is more distant. These authors were able to detect immunological differences between subspecies of *Uria aalge* and *U. lomvia*.

Judin (1965) proposed a classification of the shorebirds based on anatomy and including data from his studies on jaw musculature and the propatagial tendons. He allocated the Gruiformes, Charadriiformes, and Columbiformes to a superorder Charadriornithes. Within the Charadriiformes he recognized three suborders: Jacanae, Limicolae (Rostratulidae, Charadriidae), and Laro-Limicolae (Glareolidae, Pluvianidae, Chionidae, Thinocoridae, Dromadidae, Stercorariidae, Laridae, Alcidae).

The thigh muscles of three scolopacids, namely, *Limnodromus griseus*, *Capella* (= *Gallinago gallinago*) and *Tryngites subruficollis* were dissected by T. Fleming (1966). The three species were quite similar and no conclusions concerning relationships were presented.

R. Brown, Jones, and Hussell (1967) found that the Sabine's gull (*Larus sabini*) is similar to other gulls in its breeding behavior, yet enough differences exist to set *L. sabini* apart. The writers believed that some of the behavioral peculiarities of this species may be related to its breeding in small, loose groups on the flat tundra during the short Arctic summer. They thought that Sabine's gull is most closely related to the Franklin's gull (*L. pipixcan*), and noted similarities to the swallow-tailed gull (*L. furcatus*).

Rylander (1968) compared the serum protein patterns of four sandpipers of the genus *Calidris* by starch gel electrophoresis. He found considerable intraspecific variation and was unable to distinguish among the species by this technique.

The color patterns of the downy young in the Charadrii were analyzed by Jehl (1968a). He found that these patterns may be suggestive of relationships among the genera, tribes, and families. Some of his principal taxonomic conclusions (p. 44) were:

1. The Rostratulidae are most closely allied to the Jacanidae; these families are not closely allied to other shorebird families.
2. The Burhinidae are allied to the Haematopodidae and the Recurvirostridae.
3. There is no evidence to link *Ibidorhyncha* most closely to the Recurvirostridae.
4. The Glareolidae are closely allied to the Charadriidae. *Peltohyas* is a courser; *Rhinoptilus* may not be a natural taxon.
5. The Charadriidae are allied to the Recurvirostridae and Haematopodidae. *Phegornis* is a plover.
6. The Scolopacidae, which do not seem to be closely allied to the Charadriidae, comprise six subfamilies.

Jehl (1968b) reviewed the classification of the surf bird (*Aphriza virgata*) and from the plumage pattern of the downy young supported its inclusion in the subfamily Calidridinae of the Scolopacidae.

Sibley, Corbin, and Ahlquist (1968) reviewed the opinions regarding the relationships of the seedsnipe (Thinocoridae) and compared the starch gel electrophoretic patterns of the hemoglobins and egg white proteins of the Thinocoridae with those of all other groups that have been proposed as close relatives. Both protein systems gave patterns for the seedsnipe which were most similar to those of the Charadriiformes, but it was not possible to decide to which charadriiform group the seedsnipe are most closely allied.

Three stages of adaptive radiation of the Alcidae were defined by Bédard (1969). Unlike Storer (1945b) he considered *Endomychura* and the other small plankton-feeding species to be specialized. An opposite trend is represented by the primarily fish-eating forms like *Uria* and *Alca*. The puffins (*Fratercula*, *Lunda*, *Cerorhinca*) and an auklet (*Cyclorhynchus*) feed on both fish and plankton and show intermediate adaptations. Bédard's analysis was based mainly on the structure of the bill and the tongue.

Hudson et al. (1969) made numerical comparisons among the species of the suborders Lari and Alcae based upon 56 characters of the pectoral musculature and 52 of the pelvic musculature. These authors considered the skuas to be more specialized in the leg musculature and the gulls to be more specialized in the wing musculature, and they recognized the subfamilies Stercorariinae, Larinae, and Sterninae in the Laridae. *Rynchops*, they believed, shows enough peculiarities in its musculature to warrant family status. They also felt that the Alcidae should be placed in a separate suborder and regarded *Alca* and *Uria* as being more specialized than the puffins.

Schnell (1970a,b), in a phenetic study of the suborder Lari, compared 51 skeletal and 72 external characters among 93 species of the Stercorariidae, Laridae, and Rynchopidae. He used multivariate statistical techniques and generated a number of phenograms by treating his data in various ways. In most characters *Rynchops* seemed to be most similar to the terns. Schnell also felt that the differences between jaegers and gulls were greater than those between gulls and terns. He was unable in most cases to obtain clusters of species within the gulls or terns and was impressed by the uniformity of both of these groups.

SUMMARY

The Jacanidae have been thought to be allied to the shorebirds, the Rallidae, the Eurypygidae, and Rhynochetidae. The Rostratulidae have usually been considered charadriiform, and, among several groups, the Jacanidae and Scolopacidae frequently

have been proposed as their nearest allies. The Haematopodidae, Charadriidae, Scolopacidae, Phalaropodidae, and Recurvirostridae are thought by most to represent a closely related unit. These families formed the Limicolae of many authors. The closest relatives of these families are a matter of debate, as is the allocation of certain problematic genera.

The Dromadidae and the Glareolidae have also been most often placed in the Charadriiformes, but whether they are closer to the pluvialine or larine lines of evolution is uncertain. The Galliformes, Turnicidae, Pteroclididae, and Chionididae have been proposed as the nearest relatives of the Thinocoridae. Few authorities have disputed that the gulls, terns, and jaegers form a closely knit group and the Procellariiformes have often been suggested as their nearest allies outside the charadriiform assemblage. *Rynchops* is larine, but there is no agreement concerning its relationships to either the gulls or the terns.

The consensus is that the Alcidae are Charadriiformes, but they have also been placed with the loons and grebes, the penguins, and the diving petrels.

The historical review leads to the suggestion that the Charadriiformes, as defined by Wetmore (1960), are probably monophyletic, yet the relationships among many of the constituent groups are obscure. Of other avian orders the Gruiformes, Sphenisciformes (via the Alcidae), Columbiformes (via *Pterocles*), Gaviiformes, and Procellariiformes have been proposed as being allied to the Charadriiformes.

THE EGG WHITE PROTEIN EVIDENCE

ORDER CHARADRIIFORMES

FAMILY JACANIDAE, Jacanas or Lilytrotters. 2/7, fig. 20.

Species examined: *Actophilornis africanus*; *Jacana spinosa*.

FAMILY ROSTRATULIDAE, Painted-Snipe. 2/2, fig. 20.

Species examined: *Rostratula benghalensis*; *Nycticryphes semicollaris*.

FAMILY HAEMATOPODIDAE, Oystercatchers. 2/6, fig. 20.

Species examined: *Haematopus ostralegus*, *fuliginosus*.

FAMILY CHARADRIIDAE, Plovers. 20/56, figs. 20, 21.

Species examined (nomenclature follows W. Bock, 1958): *Vanellus vanellus*, *armatus*, *spinus*, *tectus*, *melanopterus*, *coronatus*, *senegallus*, *chilensis*, *tricolor*, *miles*; *Pluvialis dominica*, *squatarola*; *Charadrius hiaticula*, *dubius*, *vociferus*, *pecuarius*, *alexandrinus*, *melanops*, *cinctus*; *Eudromias morinellus*.

FAMILY SCOLOPACIDAE, Snipe, Woodcock, Sandpipers. 25/86, figs. 21, 22.

Species examined (nomenclature based on British Ornithologists' Union, 1952; Stout, 1967; Jehl, 1968a): *Limosa limosa*, *haemastica*, *fedoa*; *Numenius phaeopus*, *arquata*, *americanus*; *Tringa totanus*, *flavipes*; *Catoptrophorus semipalmatus*; *Actitis hypoleucos*, *macularia*; *Arenaria interpres*; *Gallinago gallinago*, *paraguaiiae*; *Limnodromus griseus*, *scolopaceus*; *Calidris canutus*, *alba*, *pusilla*, *minutilla*, *bairdii*, *maritima*, *alpina*; *Limicola falcinellus*; *Philomachus pugnax*.

FAMILY RECURVIROSTRIDAE, Avocets, Stilts. 4/7, fig. 22.

Species examined: *Himantopus himantopus*; *Recurvirostra avocetta*, *americana*, *novaehollandiae*.

FAMILY PHALAROPODIDAE, Phalaropes. 3/3, fig. 22.

Species examined: *Phalaropus fulicarius*, *lobatus*, *tricolor*.

FAMILY DROMADIDAE, Crab-plover. 0/1.

FAMILY BURHINIDAE, Thick-knees. 3/9, fig. 22.

Species examined: *Burhinus oedicephalus*, *capensis*, *bistriatus*.

FAMILY GLAREOLIDAE, Pratincoles, Coursers. 6/16, fig. 22.

Species examined: *Cursorius cursor*; *Rhinoptilus africanus*; *Peltohyas australis*; *Stiltia isabella*; *Glareola pratincola*, *cinerea*.

FAMILY THINOCORIDAE, Seedsnipe. 3/4, fig. 23.

Species examined: *Attagis gayi*; *Thinocorus orbignyianus*, *rumicivorus*.

FAMILY CHIONIDIDAE, Sheatbills. 1/2, fig. 23.

Species examined: *Chionis alba*.

FAMILY STERCORARIIDAE, Jaegers, Skuas. 3/4, fig. 23.

Species examined: *Stercorarius skua*, *parasiticus*, *longicaudus*.

FAMILY LARIDAE, Gulls, Terns. 46/82, figs. 23-25.

Species examined (nomenclature follows Moynihan, 1959b): *Larus atricilla*, *pipixcan*, *modestus*, *heermanni*, *tridactylus*, *philadelphia*, *ridibundus*, *cirrocephalus*, *novaehollandiae*, *furcatus*, *sabini*, *crassirostris*, *pacificus*, *delawarensis*, *canus*, *argentatus*, *thayeri*, *fuscus*, *dominicanus*, *marinus*, *glaucescens*, *hyperboreus*; *Rynchops nigra*; *Anous stolidus*, *tenuirostris*, *ceruleus*, *albus*; *Larosterna inca*; *Sterna nilotica*, *caspia*, *maxima*, *bergii*, *elegans*, *dougalli*, *sumatrana*, *hirundo*, *vittata*, *paradisaea*, *forsteri*, *lunata*, *fuscata*, *hybrida*, *leucoptera*, *nigra*, *albifrons*, *lorata*.

FAMILY ALCIDAE, Auks, Murres, Puffins. 9/22, fig. 25.

Species examined: *Plautus alle*; *Alca torda*; *Uria lomvia*, *aalge*; *Cephus grylle*, *columba*; *Ptychoramphus aleuticus*; *Lunda cirrhata*; *Fratercula arctica*.

Although the starch gel patterns of the Charadriiformes are remarkably uniform, there are some minor differences which permit the recognition of several pattern types within the order.

The simplest pattern is shared by the Charadriidae, Glareolidae, *Chionis*, *Stercorarius*, *Rynchops*, Laridae, and Alcidae. In this pattern Component 18 moves about 1.0 cm toward the anode. Component 18 usually is more concentrated than any of the conalbumin bands, which migrate either cathodally or anodally to Component 18. The position of the conalbumins varies within families and even genera and appears to be of little taxonomic value in these groups. The variation in conalbumins is probably due to one or more of the following: genetic polymorphism, differential binding of iron or buffer ions, or conformational changes due to partial denaturation during storage.

The ovomucoid migrates 5.0 cm or more anodally from the origin. It is a broad band, nearly as concentrated as the ovalbumin, and is not subdivided. The ovalbumin, which migrates about 7.0 cm anodally, is also a broad band, more rectangular than oval in shape. Even in dilute samples the ovalbumin appears to have only a single component.

The variation in the mobilities of the ovomucoids and albumins in the patterns of these charadriiform groups is slight. Thus, there is little in the patterns to separate the families or to indicate relationships *inter se*.

The egg white patterns of *Haematopus*, *Himantopus*, *Recurvirostra*, *Numenius*, and *Burhinus* are similar to the main type in all respects except that they have a dense, well-defined prealbumin that migrates just anodally to the ovalbumin. The significance of this difference is not known.

The patterns of the Scolopacidae (including *Arenaria*) and the Phalaropodidae differ somewhat from the main charadriiform pattern. The conalbumin bands are usually more concentrated than, e.g., those of the plovers or gulls, but the variation in mobility is the same. The ovomucoid is less concentrated and migrates less far anodally. It is often subdivided into two or more components. The patterns of *Gallinago gallinago* and *Phalaropus lobatus* (figs. 21, 22) are good examples of multiple

bands in the ovomucoid region. The pattern of *Numenius* agrees with those of the other Scolopacidae in having a multiple ovomucoid.

The patterns of the sandpipers and phalaropes differ from the main charadriiform pattern in having one or more prominent bands in the "globulin" region, but all groups have identical mobilities of their ovalbumins.

The patterns of the Thinocoridae fit within the range of variation among the Charadriiformes but are not identical to those of any group. In the pattern of *Attagis gayi* the three conalbumins migrate cathodally; in the pattern of *Thinocorus orbignyianus* only one does. This is not a considerable difference because *Anous albus*, *Alca torda*, and *Cepphus columba* have at least one cathodally migrating conalbumin. The patterns of *Attagis* and *Thinocorus* differ slightly in the mobilities of their ovomucoids. *Attagis* appears to have two ovalbumin fractions and *Thinocorus* has but one. Comparisons to the patterns of groups outside the Charadriiformes reveal few striking similarities; thus, we concur with the observations of Sibley, Corbin, and Ahlquist (1968).

The patterns of the Jacanidae and Rostratulidae agree with each other and differ from those of other charadriiforms in having a cathodally migrating lysozyme component. This band is very faint in the patterns of *Rostratula* and *Jacana*, stronger in *Nycticryphes*, and strongest in *Actophilornis*. The conalbumins are more numerous than in other shorebirds—five or six bands can be detected with certainty. The position of the conalbumins varies, no two of the four genera being alike. In the middle region of the pattern, in both painted snipe and jacanas, are two bands which may represent ovomucoids. The ovalbumin in the pattern of both groups has the same mobility as that of other Charadriiformes. In dilute samples *Nycticryphes* has two bands in the ovalbumin region, similar to the condition found in *Attagis* and *Numenius*. The patterns of the Rallidae differ from those of the Jacanidae and Rostratulidae mainly in having multiple ovalbumins of slower mobility. There are also differences in the details of other aspects of the pattern. Among Gruiformes, only the bustards have a prominent lysozyme in their patterns, but they also have an ovalbumin of higher mobility and different shape than those of the Jacanidae or Rostratulidae. Other regions of the pattern also differ. In summary, the patterns of the Jacanidae and Rostratulidae, although charadriiform, are more similar to each other than either is to the pattern of another group of Charadriiformes.

The resemblances of the charadriiform egg white pattern to the patterns of such groups as the Gaviiformes, Procellariiformes, Phaethontidae, and Fregatidae have already been mentioned. Comparisons among the patterns of the Charadriiformes and the Columbiformes, particularly the Pteroclididae, are made in the section on the latter order. Of other non-passerine groups, only the main assemblage of Gruiformes (e.g., Rallidae, Gruidae, Aramididae, Heliornithidae, Eurypygidae) resemble those of the shorebirds. The general arrangement and mobilities of the components are similar, the main difference being the multiple ovalbumin of the pattern of the Rallidae. Thus, although the egg white evidence does not strongly support a gruiform-charadriiform relationship, neither can the possibility of such an alliance be discounted.

CONCLUSIONS

The Charadriiformes are a closely related assemblage of birds that have radiated into a number of adaptive zones and have become quite diverse in external characteristics. The egg white protein evidence, other than underscoring the basic uniformity, does not clarify many relationships within the order, but some possible alliances are

suggested. The Jacanidae and Rostratulidae may be more closely related to each other than either is to any other group of Charadriiformes. The Scolopacidae may be more distinct from the Charadriidae than has often been thought. The Alcidae are more closely related to the Laridae and other Charadriiformes than they are to the Gaviidae, Spheniscidae, or the Pelecanoididae. Relationships within the Charadriiformes need to be clarified by additional studies.

The nearest relatives of the Charadriiformes are probably the Pteroclididae, Procellariiformes, Gruiformes, and Gaviiformes.

ORDER COLUMBIFORMES

Suborder Pterocletes

Family Pteroclididae, Sandgrouse

Suborder Columbae

Family Raphidae, Dodos, Solitaires (extinct)

Family Columbidae, Pigeons, Doves

Wetmore, 1960

INTRODUCTION

The family Pteroclididae contains 16 species in two genera. The two species of *Syrnhaptēs* occur in the arid steppes of central Asia, and the 14 species of *Pterocles* are found mainly in Africa, with representatives extending to India, central Asia, southern Russia, southern France, and the Canary Islands.

The relationships of the sandgrouse are one of the most debated questions in avian systematics. The Pteroclididae share several seemingly important characters with the Columbidae but also differ in many ways. The sandgrouse also show resemblances to the charadriiforms and the galliforms. Many of the characters of the sandgrouse are adaptive responses to life in an arid environment and such specializations tend to obscure the comparability to other groups. This debate involves the usual puzzle of the interpretation and weighting of characters, i.e., of convergence versus common ancestry.

The 289 species of the Columbidae seem to constitute an unquestionably natural group although there is a moderately high degree of adaptive diversity within the family. They have had a long, complex evolutionary history and, like the parrots, may once have been a dominant, cosmopolitan group that has declined somewhat with the rise of the Passeriformes (Darlington, 1957: 272). The pigeons and doves are easily distinguished from other groups but their nearest relatives are still in doubt. The parrots, gallinaceous birds, shorebirds and the sandgrouse have most frequently been suggested as close relatives but a clear decision among them is not yet available.

The principal questions concerning the Columbiformes are the following:

1) Are the Columbidae most closely related to the Pteroclididae, the Psittacidae, the galliforms or the charadriiforms?

2) Are the Pteroclididae most closely related to the Columbidae, the Charadriidae, the Thinocoridae, the Turnicidae, or the Phasianidae?

HISTORICAL REVIEW OF THE CLASSIFICATION

Nitzsch (1840) found pterylographic similarities between pigeons and sandgrouse and included both in the "Columbinae", one of eight principal divisions of birds. G. Gray (1844-49) followed earlier workers who were impressed with the external similarities of the sandgrouse to the gallinaceous birds. He placed the Pteroclididae in his order Gallinae, which included the Galliformes. Similarly, Bonaparte (1853) placed *Pterocles* with the Thinocoridae and Tinamidae in his Perdices.

Lilljeborg (1866) united the sandgrouse, seedsnipe, and sheathbills in the family Pteroclididae of his order Gallinae, which included the Crypturidae (= Tinamidae), Tetraonidae, and Phasianidae. He placed the pigeons, along with the megapodes and cracids, in another order, the Pullastrae, and recognized the families Columbidae and Didunculidae.

Parker's thoughts on the sand grouse were typically ambiguous: "The Sand-Grouse . . . although lower than the Grouse in many respects, being but little removed from the struthious type, yet are related, and that intimately to the Plovers and the Pigeons" (1864: 237).

Huxley (1867) noted that *Pterocles*, the Phasianidae, and the Turnicidae agree in having basipterygoid processes of similar form, long and slender anterior processes of the palatines, small maxillopalatines, and imperfectly developed vomers. He included the sandgrouse in his Alectoromorphae and thought that they connected the gallinaceous birds to the pigeons. Of the Columbidae Huxley (1867: 460) wrote: "The relations of the Peristeromorphae [pigeons and doves] with the Alectoromorphae are very close. On the other hand they seem to be allied with the Owls and the Vultures."

Huxley (1868b) altered his opinion regarding the sandgrouse and furnished additional details (p. 302-03) on their anatomical similarities to the pigeons and gallinaceous birds:

In almost all those respects in which the Grouse differ from the Fowls they approach the Pigeons; and an absolute transition between these groups is effected by the *Pteroclididae*, whose popular name of 'Sand-Grouse' might fitly be exchanged for that of 'Pigeon-Grouse.'

1. I find the vertebrae in the cervical, dorsal, lumbar, and sacral regions to have the same number in *Pterocles* and *Syrnhaptes* as in the *Alectoromorphae*; and ankylosis takes place in the same manner. . . .

2. In the skull, the palatines, the maxillo-palatines, and the mandibles resemble the corresponding parts in the *Alectoromorphae*; the pterygoid and the basipterygoid processes, on the other hand, are like those of the *Peristeromorphae*.

3. The sternum and furcula, as well as the coracoid (in its shortness, breadth, and the presence of a subclavicular process), are completely Peristeromorphic; and so is the whole fore limb.

4. The pelvis has resemblances both to that of the Grouse and that of the Pigeons, but has some peculiarities of its own.

5. The foot contrasts strongly with that of the Pigeons in its extreme brevity of the tarsometatarsus and toes, and in the reduction of the hallux, but may be regarded as an exaggeration of that of the Grouse. . . .

Thus the *Pteroclididae* are completely intermediate between the *Alectoromorphae* and the *Peristeromorphae*. They cannot be included within either of

the groups without destroying its definition, while they are perfectly definable in themselves. Hence, I think, the only advisable course is to make them into a group by themselves, of equal value with the other two, under the head of *Pterocloromorphae*.

Garrod (1874b) found the skull of *Pterocles* to be like "that of a Pigeon modified by the effects of a Grouse-like life" (p. 254). Other aspects of the anatomy of *Pterocles* indicating to Garrod an affinity to the Columbidae include the shape of the humeral head, sternum, and obturator internus muscle, and characters of the pelvis and pectoral musculature. Garrod emphasized that in all these characters *Pterocles* differs from the gallinaceous birds and did not hesitate to place the sandgrouse in a family in his Columbidae.

Garrod (1874b) used the size of the caeca, presence of the ambiens muscle, oil gland, gall bladder, and the scutellation of the tarsus to classify the Columbidae. His arrangement (with the addition of the genera of Peters, 1937) is summarized as follows:

Family Columbidae

Subfamily Columbinae (*Columba*, *Streptopelia*, *Macropygia*)

Subfamily Phapinae (*Columbigallina*, *Metriopelia*, *Zenaida*, *Zenaidura*, *Caloenas*, *Turtur*, *Tympanistria*, *Ocyphaps*, *Leucosarcia*, *Phaps*, *Ducula*, *Lopholaemus*, *Didunculus*)

Subfamily Treroninae (*Gallilolumba*, *Starnoenas*, *Geopelia*, *Treron*, *Ptilinopus*, *Goura*)

Family Pteroclididae (*Pterocles*, *Syrrhaptes*)

Elliot (1878: 234) stated: The natural position of the Pteroclididae . . . in the Class Aves, is between the Columbidae . . . on the one hand, and the Tetraonine series of the Gallinaceous birds . . . on the other. . . ." He found that "in some of their characters they are also pluvialine, and their flight is especially Plover-like . . ." (p. 235). Elliot also made the apparently unsubstantiated report that the sandgrouse drink by "sucking" or "pumping" as do pigeons, and thereby started what was to be a long and somewhat ridiculous debate.

The Columbidae of P. Sclater (1880) included both pigeons and sandgrouse, and he saw similarities between the latter and the gallinaceous birds, especially the grouse. He recognized four families of pigeons, the Carpophagidae (fruit pigeons), Gouridae (*Goura*), Didunculidae (*Didunculus*), and Columbidae. Within his order Cursorae, which included many gruiform and charadriiform groups, Reichenow (1882) erected a suborder Deserticolae to contain the Thinocoridae, Turnicidae, and Pteroclididae. His arrangement of the Columbidae was similar to Sclater's except that he recognized a family Geotrygonidae for most primarily ground-dwelling pigeons.

Gadow (1882) studied the sandgrouse with emphasis on their pterylography, osteology, myology, visceral anatomy, and natural history. He called attention to Elliot's apparent error regarding the drinking behavior of the birds, and thus established the opposite position in the argument: "The Sand-Grouse differ greatly from the Pigeons in their mode of drinking. It is well known that the latter, during the act of drinking, dip their bills into the water as far as the cleft of the mouth, and then suck the water in without raising their head till they have finished drinking. *Pterocles* and *Syrrhaptes*, on the other hand, drink as Fowls and other birds do, by taking up water mouthful by mouthful and letting it run down the throat" (p. 329).

Concerning the affinities of the sandgrouse Gadow concluded (p. 331): "No doubt Sand-Grouse are more nearly allied to the Rasores [Galliformes] than the pigeons are. Consequently we must seek for their root between the Rasorial and

Columbine branch. . . . Again, the Sand-Grouse are more clearly allied to the pigeons than to the Plovers; thus their branch must be put nearer to the Columbine branch than to that of the Plovers.”

Elliot (1885: 235) summarized the evidence for the relationships of the Pteroclididae as he interpreted it:

The sand-grouse . . . are now elevated to a distinct order, lying between the Alectoromorphae [Phasianidae *sensu lato*] on the one hand and the Peristeromorphae [Cracidae, Megapodiidae] on the other. They resemble the first of these great groups in their skull, palatines, maxillopalatines, and bill; and the second in their pterygoid and basipterygoid processes, sternum, furcula, coracoid, and fore-limbs. The feet with its short hallux, entirely wanting in *Syrnophanes*, and the short tarso-metatarsus, are very unlike a pigeon's. The vocal organs are pigeon-like; the trachea is cartilaginous, with a pair of laryngeal muscles at its bifurcation; but the crop, gizzard, gall bladder, and small intestines are those of gallinaceous birds. The *caeca coli* are voluminous, and have twelve continuous longitudinal folds in their mucous membrane. The pterylosis differs somewhat from that of the pigeon. The lateral neck-spaces reach only to the beginning of the neck; the superior wing-space is absent; the lumbar tracts coalesce with the posterior part of the dorsal tract, and the latter joins the plumage of the tibia. The sand-grouse possess an aftershaft on the contour feathers, thus differing from the pigeons, and, unlike the gallinaceous birds, have a naked oil-gland. In some characters these birds are plover-like, but they drink like a pigeon, thrusting the bill up to the nostril into the water, and retaining it there until the thirst is satisfied.

Elliot did not speculate on the relationships of the pigeons, which he treated as a separate order, the Columbidae, placed between the Pterocletes and Accipitres and arranged in five families: Didiidae (dodo and solitaire), Didunculidae (*Didunculus*), Gouridae (*Goura*), Columbidae (most typical pigeons and doves), and Carpophagidae (*Alectroenas*, *Treron*, *Ptilinopus*, *Ducula*, and other fruit pigeons).

Goodchild (1886) commented on similarities between plovers and pigeons in the arrangement of their secondary coverts and noted that the sandgrouse differ from the pigeons in this character. In a later paper (1891) he altered his interpretation of the evidence. Of the sandgrouse he concluded, "I do not see anything whatever in the style of the wing coverts in this group to warrant its being separated far from the true pigeons" (p. 328). He found a number of similarities between *Goura* and the Cracidae and Megapodiidae.

Fürbringer (1888) included both pigeons and sandgrouse in his "intermediate suborder" Columbiformes. He believed that the Columbiformes stood between the Charadriiformes and the Galliformes and that they were also not distantly allied to the Psittaciformes.

Seebohm (1888b) was convinced that the sandgrouse are intermediate between the pigeons and gallinaceous birds. He retained them in a separate order, but later (1890a) included them in his Columbidae. Additional study led Seebohm (1895) to doubt a sandgrouse-galliform relationship and to suggest that they linked the pigeons with the shorebirds. He regarded the pigeons as "the tree-perching contingent of the Charadriiformes" (p. 18).

In two papers Shufeldt (1891a,e) examined the classification of North American Columbidae. He thought that *Zenaidura* and *Columba* are closely related and do not require separate subfamily status, but that *Starnoenas* deserves such rank. A decade later Shufeldt (1901f) divided his superfamily Columboidea into three families—Gouridae (*Goura*), Carpophagidae (fruit pigeons), and Columbidae (typical pigeons

and doves). He considered the sandgrouse to be osteologically intermediate between pigeons and grouse but also noted that "the plovers are not far in another direction, and *Tinamus* and *Hemipodius* [= *Turnix*] have also distant claims to kinship" (p. 508).

The osteology, particularly of the skull, of *Pterocles* and *Syrhaptus* was studied by Shufeldt (1901a). He found similarities to both the pigeons and gallinaceous birds and suggested that the sandgrouse be treated as a "suborder" between the two groups. He did not mention any comparisons to the shorebirds or other groups. In his 1904 classification Shufeldt recognized a "super suborder" Pteroclidiformes for the sandgrouse, which he placed between the Galliformes and Columbiformes.

Although Gadow (1893) believed that the closest relatives of the pigeons are the sandgrouse, he expressed the opinion that the sandgrouse are also related to the shorebirds, and concluded (p. 209):

Die Pteroclididae könnten als 'Steppentauben' gekennzeichnet werden. Ihre unteren Verwandten sind noch indifferente Limicolae, ihre höheren, aber durchaus nicht directen Nachkommen sind die Tauben. Die Aenlichkeiten mit den Hühnern beruhen auf Analogien, oder sie gehen sehr weit zurück, sodass sie als nicht maassgebend auszuscheiden sind.

Aus irgend einer der jetztigen Familien der Limicolae lassen sich die *Pterocles* übrigens nicht ableiten. Kropf und Blinddärme wie bei *Thinocoridae* werden analoge Gebilde sein. Die Darmlagerung, die wie bei vielen Tauben vorhandene Spina interna und die Nares imperviae sichern den *Pterocles* eine den Limicolae gleichwerthige Stellung. Darmlagerung und Blinddärme, Syrinx und Eier machen sie ferner den *Columbae* gleichwertig.

The essence of Gadow's statement, but not a literal translation, is as follows: The Pteroclididae may be called "steppe pigeons." Their ancestors are still the generalized shorebirds; their next relatives, but by no means direct descendants, are the pigeons. The ties with the gallinaceous birds seem to be based upon analogy, or they go so far back that they cannot be regarded as conclusive proof of relationship. It is not possible, however, to derive the Pteroclididae from some of the extant families of shorebirds. The crop and caeca are developed for the same reasons as in the *Thinocoridae*. As in many pigeons, the intestinal coiling, the presence of an internal spine of the sternum, and the impervious nares guarantee to the sandgrouse a rank equivalent to that of the Limicolae. In the same way, the caeca and some aspects of the intestinal coiling, the syrinx, and the eggs make them more distant from the *Columbae*.

Gadow arranged the *Columbidae* into several subfamilies, with their constituents as follows: *Didunculinae* (*Didunculus*), *Treroninae* (*Treron*, *Ptilinopus*, *Ducula*, *Otidiphaps*), *Caloenadinae* (*Caloenas*), *Columbinae* (typical pigeons and doves), *Gourinae* (*Goura*).

Meade-Waldo (1896, 1897, 1906, 1922) was apparently the first to observe the unusual method by which adult sandgrouse transport water to their young by saturating their abdominal feathers at watering places and flying back to the nest. His observations were on both captive and wild *Pterocles* of several species but they were disbelieved by subsequent workers and only recently reconfirmed (see below).

Beddard (1898a: 318-19) took issue with Huxley's interpretation of the anatomical evidence bearing on the relationships of the sandgrouse. He argued:

The at least 'pseudo-holorhinal' nostrils have their counterpart among the Limicolae, in *Thinocorus*, and in some others. The solid ectethmoids too are also seen in that group, while Garrod's remark that the *Alcae* have a humerus like that of

the Columbæ and *Pterocles* is suggestive in the light of the unquestionable likeness of the Alcæ for the Limicolæ, though the actual weight of this character may be thought by some to be discounted by the fact that it is met with in the Psittaci.

Moreover *Otis*, which is to be placed somewhere near the Limicolæ, has the gallinaceous union between the squamosal and the post-frontal process, to which I have referred as possibly affining the Pterocletes to the Galli. Other characters too, which appear at first sight to be arguments in favour of the position taken up by Huxley, may be interpreted fairly as marks of affinity with the Limicolæ (and their immediate allies). Such are, for example, the long caeca (with folds in the bustards), the crop (present in *Thinocorus*), the gall bladder, &c.

It is at any rate clear that the Pterocletes occupy a lower place than the Columbæ—that *they* have given rise to the Columbæ, and not *vice versa*. The justice of this view is shown by the long caeca, the existence of an aftershaft, the complete muscle formula of the leg, and by a few other equally unmistakable characters. . . . It seems reasonable to look upon the Pterocletes as not far from the stock which produced the Limicolæ, which itself was possibly not far again from the primitive gallinaceous stock.

Mitchell (1901a) pointed out that the intestinal tracts of *Pterocles* and the pigeons are "extremely similar, and there is no indication of any affinity with the conformations exhibited in the other Charadriiformes or Gruiformes" (p. 240).

The skeletons of 70 species of pigeons and doves representing the principal groups were compared by R. Martin (1904). He discussed the phylogeny of the Columbiformes and proposed the following classification (p. 182):

Order Columbiformes

Suborder Didi

Family Dididae

Family Pezophabidae

Suborder Columbæ

Family Columbidae: Columbinae, Caloenadinae

Family Peristeridae: Peristerinae, Phabinae, Ptilopodinae.

Family Treronidae: Treroninae

Family Carpophagidae: Carpophaginae, Gourinae, Otidiphabinae

Family Didunculidae: Didunculinae.

Dubois (1902-04) recognized five families for the pigeons, with included genera as follows:

Treronidae

Treroninae (*Treron*)

Ptilopodinae (*Ptilinopus*, *Alectroenas*, *Megaloprepia*)

Carpophaginae (*Ducula*, *Lopholaemus*, *Hemiphaga*)

Columbidae

Columbinae (*Columba*)

Macropygiinae (*Turacoena*, *Macropygia*, *Reinwardtoena*)

Peristeridae

Zenaidinae (*Zenaida*, *Nesopelia*)

Turturinae (*Streptopelia*)

Geopeliinae (*Geopelia*, *Scardafella*)

Chamaepeliinae (*Columbina*, *Columbigallina*, *Claravis*, *Metriopelia*)

Phabinae (*Oena*, *Turtur*, *Chalcophaps*, *Henicophaps*, *Phaps*, *Petrophassa*, *Geophaps*, *Lophophaps*, *Ocyphaps*)

Geotrygoninae (*Aplopelia*, *Leptotila*, *Geotrygon*, *Gallicolumba*, *Leucosarcia*, *Trugon*, *Otidiphaps*, *Starnoenas*)

Gouridae (*Goura*)

Didunculidae (*Didunculus*)

Chandler (1916: 362) concluded:

The Pteroclo-columbae, according to their feather structure, show more similarities to the gallinaceous birds than to any other group. The shape of both distal and proximal barbules, and the specialized nature of the down, are all points of striking likeness. The occurrence in the tinamous, which are undoubtedly a specialized group of gallinaceous birds, of both the columbid and galline type of down, might be considered a further bond of union between the two latter groups. They show the same affiliation to some of the gruiform birds as do the gallinaceous birds, and the latter show some affinity to the Cuculiformes, especially in the presence of prongs on the hooklets of the distal barbules of back and breast feathers. The relation of the Pteroclo-columbae to the Laro-limicolae, if there is any close relationship, is not shown at all in the structure of the feathers. The Pterocles show a number of differences from the Columbidae in feather structure, which are probably specializations of their own, and do not show closer approximation to any other group.

W. D. Miller (1924) summarized the data on the condition of the fifth secondary and noted that both eutaxic and diastataxic species occur in the Columbidae. (See section on the fifth secondary in the Introduction to the present volume.)

Bowen (1927) revised the genera of sandgrouse based on the time at which they drink at water holes. He found that some species drink early in the morning and late afternoon while others are crepuscular. He felt that this was a better basis for defining genera than external characteristics.

Waterston (1928), who compared the mallophagan parasites of the sandgrouse with those of pigeons and gallinaceous birds, concluded (p. 336): "*Syrhoptoecus* has not, in my opinion, any close affinities with any of the Philopteridae found on Pigeons (Columbidae), though the latter family also, judged by its parasites, is related only to the galline group. Sand-Grouse and Pigeons must stand rather apart within this complex, and the position of the first-named would appear to be between the Grouse and the Pheasants."

E. Stresemann (1927-34) maintained the pigeons and sandgrouse in separate but adjacent orders. On the basis of the skull, pelvic structure, and musculature he considered the two groups to be certainly but still very distantly allied. He also repeated the assertion that the sandgrouse drink like pigeons.

The sandgrouse were placed in a suborder of the Columbiformes by Peters (1937) and Wetmore (1930, 1934). Peters recognized four subfamilies in the Columbidae: Treroninae (*Treron*, *Alectroenas*, *Ptilinopus*, *Ducula*, and other fruit pigeons), Columbininae (typical pigeons and doves), Gourinae (*Goura*), Didunculinae (*Didunculus*).

G. Niethammer (1934) examined the morphology and histology of the crop of *Pterocles orientalis* and made comparisons with pigeons and gallinaceous birds. In most characters the structure of the crop is more like that of pigeons than that of the Galliformes, but enough differences between *Pterocles* and *Columba* exist so that Niethammer agreed with the separation of the sandgrouse into a separate family. No comparisons involving other groups were made.

Irwin and his colleagues have written a series of papers on the antigenic properties of the red blood cells of a number of species of Columbidae. Some of the papers pertaining to systematic problems are as follows: Bryan (1953); Bryan and Irwin

(1961); Bryan and Miller (1953); Cumley and Cole (1942); Cumley and Irwin (1940; 1941a,b; 1942a,b; 1944; 1952); Cumley, Irwin, and Cole (1942, 1943); Gershowitz (1954); Irwin (1932a; 1938; 1939; 1947; 1949a,b; 1951; 1952; 1953; 1955); Irwin and Cole (1936a; 1937; 1940; 1945a,b); Irwin, Cole, and Gordon (1936); Irwin and Cumley (1940, 1942, 1943, 1945, 1947); Irwin and Miller (1961); Jones (1947); W. J. Miller (1953a; 1954; 1956; 1964); W. J. Miller and Bryan (1951, 1953); Palm (1955); Palm and Irwin (1957, 1962); Stimpfling and Irwin (1960a,b). Although the writers were mainly interested in immunogenetics, many of the papers are of taxonomic interest. The details of these investigations are beyond the scope of this paper, but we will summarize the pertinent points.

Irwin (1932a) found that two thirds of the antigenic specificities possessed by *Streptopelia chinensis* were not present in the red cells of *S. risoria*. In contrast, only one sixth of the antigenic specificities of *risoria* red cells were not also shared with *chinensis*. It was clear that antisera specific to only one or a few of the antigenic specificities of a species could be prepared by absorbing the anti-red cell antiserum of species A with the red cells of species B. In this way only the species-specific antibodies of species A remained in the antiserum, which could then be reacted with the red cells of other species. By making reciprocal tests using various antisera absorbed with the red cells of different species, it was possible to determine the extent to which the various red cell antigens and their specificities were shared among the species studied. The assumption was made that species of closer genetic relationship will have more similar antigens, and conversely.

Cumley and Cole (1942) and Cumley and Irwin (1944) found a correlation between the geographic distribution of the species of *Columba* and the red cell antigenic specificities possessed by the respective species. A series of antigens was specific to the Old World species, another group was shared by the New World forms. Only a few antigens were common to only one or two species of both the Old and New Worlds. These authors were also able to define clusters of apparently more closely related species within the Old and New World groups.

Irwin's group was also able to determine some probable relationships within *Streptopelia* by the red cell antigen specificities. Irwin and his colleagues have been conservative in drawing conclusions of taxonomic importance from these data and additional inferences regarding relationships in *Columba* and *Streptopelia* can probably be made from the immunogenetic data.

Clay (1950) considered the evidence from the Mallophaga to be uninformative on the affinities of the sandgrouse. In her opinion, *Neomenopon* has no obvious relationship to other feather lice, and *Syrrhaptoecus* is a member of the widespread Degeeriellinae.

Mayr and Amadon (1951) tentatively placed their Columbace "near the Laro-Limicolae" and thought it "unlikely that the sand grouse (Pteroclididae) are grouse-like except in superficial adaptations." They also noted that "McDowell has found similarities between the humeri of parrots and those of pigeons" (p. 9).

Subdivisions of the fruit pigeon genus *Ptilinopus* based on size and color pattern were proposed by Cain (1954). Similarly, using a variety of color characters, Husain (1958) revised the genus *Treron*.

Verheyen (1957a) divided the Columbidae of Peters (1937) into three families: Caloenadidae (*Goura*, *Microgoura*, *Caloenas*, and the dodos), Duculidae (fruit pigeons), and Columbidae. Verheyen's highly fractionated classification included 68 genera (Peters recognized 59) and numerous subfamilies and tribes. The Pteroclididae were found by Verheyen (1958a) to be unlike the pigeons. He placed them in a separate order Turniciformes along with the Mesitornithidae, Turnicidae, Pedionomidae, and Thinocoridae. In 1961 Verheyen broke up his "transitorial" order Turni-

ciformes because "the position-principal includes ideas with reference to relationships" (p. 21). He considered the Pteroclididae and Thinocoridae to be related by "paramorphogenesis" and included them in separate suborders in his Columbiformes. He retained three families for the pigeons, as he had done previously.

Hüe and Etchécopar (1957) provided an account of the systematics and natural history of the sandgrouse. They felt that the sandgrouse are best included in the Columbiformes, but did not mention anything about drinking methods in the two groups.

Using external features, color pattern, and behavior Goodwin (1958) merged *Zenaidura*, *Melopelia*, and *Nesopelia* into *Zenaida*, and *Osculatia* into *Geotrygon*. He believed that *Starmoenas* is closely related to *Geotrygon* and that the American ground doves are more closely related to *Zenaida* than to the Old World *Gallinocolumba*. In a subsequent paper (1959a) he lumped *Columbigallina*, *Eupelia* and *Oxytelia* with *Columbina*, and *Leptophaps* and *Gymnopenia* with *Metriopelia*. Goodwin (1959b) employed a broad concept of the genus *Columba*, as had Peters (1937). He was unable to separate the New World species of *Columba* from those of the Old World. In 1960 Goodwin revised the taxonomy of the fruit pigeons of the genus *Ducula*, which he considered to be closely allied to *Ptilinopus*.

Sibley (1960) compared the egg white proteins of 31 species of columbids by means of paper electrophoresis. He found "little in the egg-white profiles to suggest clear relationships" to any other order of birds but did note that the family could be divided into groups upon the basis of variations in the electrophoretic patterns. The New World and Old World species of *Columba* were found to have mutually distinguishable egg white patterns.

C. Harrison (1960) suggested that the chestnut coloration of the primaries in certain widely dispersed species of doves indicates that these species shared a common ancestry. He proposed that the classification of Salvadori (1893), which placed the bronze-winged doves in a family Peristeridae, provided a better indication of their relationships than the arrangement of Peters (1937).

From morphological and behavioral evidence Johnston (1961) suggested that *Columbigallina*, *Scardafella*, and *Eupelia* should be merged into *Columbina*. Johnston (1962) used the condition of the tenth primary and the angle of the skull at the frontal hinge as new characters for assessing relationships in the genus *Columba*. He re-evaluated osteological and plumage characters and divided the genus *Columba* of Peters (1937) into three genera. Johnston's *Columba* contained all the Old World species plus the New World *fasciata*, *araucana*, and *caribaea*. *Oenoenas* included the New World *subvinacea*, *plumbea*, *nigrirostris*, and *goodsoni*, and *Patagioenas* contained the remaining New World forms.

In a paper on the taxonomic value of various aspects of avian behavior Wickler (1961) reported that he had filmed the drinking of a captive diamond dove (*Geopelia cuneata*) and a long-tailed grassfinch (*Poephila acuticauda*: Estrildinae) and found that their throat movements were identical. He noted that the sandgrouse, by making repeated sucks and raising the head after each, drink differently from pigeons. Wickler also remarked that the tooth-billed pigeon (*Didunculus*) drinks in the same manner as a domestic goose.

In 1964 Meinertzhagen wrote that the sandgrouse "drink like pigeons, placing the bill in the water and continuously swallowing without raising the head. . . ." He also noted: "It has been suggested that water is also carried to young in the abdominal feathers, but that is not so" (p. 712). Goodwin (1965) disagreed with Meinertzhagen and reported his own observations on captive sandgrouse, which indicate that they do not drink like pigeons. Goodwin maintained that "there is no reason for anyone to suppose that their drinking methods indicate any close relationship between sand-

grouse and pigeons. For myself I have long thought sandgrouse are probably most closely related to the true plovers to which, in spite of the differences involved in their adaptation to living in arid regions and feeding on seeds, they show many similarities, especially of behaviour" (p. 76).

Several species of waxbills (*Estrilda*, *Uraeginthus*, *Amandava*) that Goodwin observed in captivity did at times drink by "pumping" in the manner of pigeons. Doves of the genus *Streptopelia* showed variability in their drinking method depending upon the degree of thirst and whether the water was clean. This led Goodwin (p. 77) to conclude, "I think that the difference between the sucking drinking of pigeons and some others and the 'scooping up' method may not be so definite as has been implied. It seems to me probable that many birds that drink 'normally' suck as their bills go into the water and do not rely solely on scooping and gravity as sometimes appears. In some instances differences of drinking behavior have reference to different circumstances and may not therefore be a specific character when seen in two different species."

Observations by Cade, Willoughby, and Maclean (1966) on *Pterocles namaqua*, *P. burchelli* and several species of Columbidae at water holes revealed considerable differences in drinking behavior. The sandgrouse drank for 5–10 seconds, then raised the head to swallow, repeating this sequence several times. The doves all immersed their beaks in the water and drank to satiety by "pumping" before raising their heads. Cade and Greenwald (1966) reported that the mousebirds *Colius colius* and *C. indicus* drink by "pumping" as do pigeons.

Contrary to the report by Meinertzhagen (1964) and others, Cade and Maclean (1967) observed and photographed how adult male sandgrouse transport water to their young in their breast feathers. They also described the peculiarities in the structure of these feathers which permit them to retain considerably more water than the feathers of other birds. Their observations were on *Pterocles namaqua* and *P. burchelli*. U. George (1969, 1970) found similar behavior in *Pterocles senegallus* and *P. coronatus*. Thus were the original observations of Meade-Waldo confirmed and extended.

Goodwin (1967) published a monograph on the Columbidae. Although the main part of his book is concerned with natural history, Goodwin proposed relationships within the family based primarily on his studies and those of others on behavior and plumage patterns. From his linear sequence and dendrograms several groupings may be discerned (the genera in parentheses are presumed to be those most closely allied within a group):

- 1) *Columba*, *Streptopelia*, *Aplopelia*
- 2) *Macropygia*, *Reinwardtoena*, *Turacoena*
- 3) (*Turtur*, *Oena*), *Chalcophaps*, *Henicophaps*, (*Phaps*, *Ocyphaps*, *Petrophassa*), *Leucosarcia*, *Geopelia*
- 4) *Zenaida*, (*Columbina*, *Claravis*, *Metriopelia*, *Scardafella*, *Uropelia*), *Leptotila*, (*Geotrygon*, *Starnoenas*)
- 5) A loose assemblage of distinctive genera: *Caloenas*, *Gallicolumba*, *Trugon*, *Microgoura*, *Otidiphaps*, *Goura*, *Didunculus*
- 6) *Phapitreron*, *Treron*, (*Ptilinopus*, *Drepanoptila*, *Alectroenas*, *Ducula*), (*Hemiphaga*, *Lopholaimus*), *Cryptophaps*, *Gymnophaps*.

Following the clarification of the differences in drinking behavior between sandgrouse and pigeons, Maclean (1967) brought together other behavioral evidence from his field studies in support of an alliance between the sandgrouse and the shorebirds. Using moving-boundary electrophoresis Maclean also compared the egg white proteins of *Pterocles namaqua* and *burchelli* with those of the shorebirds *Actitis*, *Himantopus*, *Burhinus*, and *Rhinoptilus* and the columbids *Streptopelia* and *Zenaida*. The pat-

terns of the sandgrouse resembled those of the Charadriiformes more than they did those of the pigeons. Maclean suggested that the sandgrouse be included in the Charadriiformes as a suborder next to the Charadrii. Additional details of his field observations on sandgrouse were published separately (Maclean, 1968).

Stegmann (1968, 1969) responded to Maclean's paper with a vigorous reassertion of his belief that the sandgrouse are closely related to the pigeons. Citing his previous papers (1957a,b; 1958; 1959) on the anatomy of sandgrouse and pigeons, Stegmann brought together data from the morphology of the skull, limbs, and vertebral column in support of his view. He regarded the sandgrouse as being more advanced in some structural aspects than pigeons and felt that they have secondarily become ground-dwelling birds. He viewed the Pteroclo-Columbae as a group of considerable antiquity. In his opinion, the Charadriiformes and Galliformes, which are of more recent derivation, have developed some convergent similarities to sandgrouse.

Maclean (1969a) quickly responded and claimed that Stegmann had ignored all evidence other than morphological characters in assessing the relationships of the sandgrouse. Maclean agreed that morphologically the sandgrouse and pigeons are similar in many respects, but he took issue (p. 105) with Stegmann's assertion that the sandgrouse wing is a modified dove wing, as follows:

Since it is not disputed that sandgrouse and doves probably have a charadriiform ancestor and since the sandgrouse wing is essentially charadriiform in shape, I fail to see the necessity to derive it from a dove wing. It is both more logical and much easier to derive the sandgrouse wing directly from a charadriiform wing instead of deriving so similar a structure from the very different dove wing.

Maclean (p. 106) uncovered an apparently more fundamental error in Stegmann's insistence that the sandgrouse are secondarily terrestrial:

On the subject of the precocity of sandgrouse young, it is my opinion that the redevelopment of so highly precocial a chick from one as highly altricial as that of the doves is most unlikely. That the sandgrouse should have redeveloped so many charadriine behaviour patterns associated with ground nesting (egg coloration, clutch size, side-throwing, bobbing, chick type, nest scrape) after having been arboreal, as suggested by D. Stegmann, is asking too much of evolutionary processes and goes against the basic tenet that a feature once lost is seldom, if ever, re-acquired. . . .

There is nothing at all in the make-up of any sandgrouse to indicate an arboreal ancestry; on the contrary, the indications are that the doves also had a terrestrial ancestor, since so many of them, however arboreal their nesting habits, still feed on the ground. Those doves that nest on the ground are almost certainly secondarily terrestrial nesters, but they show no trend whatever toward the sandgrouse condition. Most of the ground nesting doves still build nests; if they do not, they make no nest scrape and do not side-throw in the charadriine way. No ground nesting dove shows any tendency toward cryptic egg coloration or toward precocial young.

Von Frisch (1969, 1970) reported several years' observations on *Pterocles alchata* in southern France. Although he presented a number of points in their behavior which seem to ally the sandgrouse to the shorebirds, he found little evidence of water transportation to the young. This latter situation may be due to a relatively greater abundance of water in the study area.

In a review of Maclean's (1969b) paper on the Thinocoridae, Olson (1970) took the opportunity to interject his opinion regarding the affinities of the sandgrouse.

Even the most perfunctory comparison of skeletons of pteroclidids will disclose that, element for element, they are scarcely distinguishable from columbids and that both differ significantly from any Charadriiform type, including the Thinocoridae. A number of other characters linking the doves and sandgrouse have been noted by several early authors. It is inconceivable that this multitude of characters is attributable to convergence.

From a comparative study of the tryptic peptides of the ovalbumins of 18 species of columbids, including 10 species of *Columba*, Corbin (1967, 1968) suggested that "the Old and New World species-groups of *Columba* appear to have evolved from a common ancestor followed by speciation in the Eastern and Western Hemispheres. Since the ovalbumins of some *Columba* species in each hemisphere are most similar to ovalbumins of *Columba* species in the other hemisphere, these data do not support the division of *Columba* into two or more genera . . ." (1968: 10-11). *Leptotila* and *Streptopelia* were most similar to *Columba* and within *Columba*, *fasciata* was most similar to other American species, especially to *flavirostris*. The Old World species *C. palumbus* was found to have an ovalbumin more similar to that of the New World species *cayennensis* than to those of other Old World species. Data from other sources however, indicate a close relationship among the Old World species *C. palumbus*, *oenas*, *guinea* and *livia*.

Timmermann (1969) reviewed the evidence from the Mallophaga bearing on the relationships of the sandgrouse. The feather lice indicate no close affinities between the pigeons and sandgrouse. He admitted that he could detect a distant, indirect alliance between the two groups only through the gallinaceous birds. He found many differences between the Mallophaga characteristic of the Charadriiformes (genera of the *Cummingssiella*-complex, *Quadriceps*, *Saemundssonina*, *Austromenopon*, *Actornithophilus*) and those of the Pteroclididae (*Syrrhaptoecus*, *Neomenopon*). To Timmermann a phylogenetic connection between the shorebirds and sandgrouse could only have existed before the birds acquired their mallophagan faunas.

SUMMARY

The gallinaceous birds, parrots, and shorebirds have been proposed as the nearest allies of the Columbiformes. The pigeons themselves show some anatomical similarities to all these groups, but the relationships to the Galliformes and Charadriiformes have been suggested as being mainly through the Pteroclididae. But the nearest relatives of the Pteroclididae, which thus become the focal point of discussion, remain in debate. Many authors attribute the resemblances between *Pterocles* and the Galliformes to convergence, but some have interpreted the evidence from the Mallophaga in favor of such an alliance. Mainly behavioral, but some morphological, evidence has been used in support of a *Pterocles*-shorebird relationship. Some morphological characters seem to suggest close ties between the sandgrouse and the pigeons, but these can be interpreted in various ways. The myth about drinking behavior, long cited in support of a relationship between sandgrouse and pigeons, has been disproved. The sum of previous studies suggests that the sandgrouse may be allied to either the shorebirds or the pigeons, or that they may in some way connect the two large orders. The Columbidae, in turn, may be related in a more distant way to the Psittaciformes.

THE EGG WHITE PROTEIN EVIDENCE

ORDER COLUMBIFORMES

FAMILY PTEROCLIDAE, Sandgrouse. 3/16, fig. 26.

Species examined: *Pterocles alchata*, *exustus*, *gutturalis*.

FAMILY COLUMBIDAE, Pigeons, Doves. 55/289, figs. 26–28.

Species examined (nomenclature follows Goodwin, 1967): *Columba livia*, *rupestris*, *guinea*, *oenas*, *palumbus*, *leucocephala*, *speciosa*, *picazuro*, *maculosa*, *fasciata*, *cayennensis*, *flavirostris*; *Streptopelia turtur*, *decaocto*, *roseogrisea*, *deci piens*, *semitorquata*, *capicola*, *chinensis*, *senegalensis*; *Aplopelia larvata*; *Turtur chalcospilos*, *abyssinicus*; *Oena capensis*; *Chalcophaps indica*; *Phaps chalcoptera*, *elegans*; *Ocyphaps lophotes*; *Petrophassa ferruginea*, *scripta*; *Geopelia striata*; *Leucosarcia melanoleuca*; *Zenaida macroura*, *auriculata*, *aurita*, *galapagoensis*, *asiatica*; *Columbina passerina*, *talpacoti*, *picui*, *cruziana*; *Claravis pretiosa*; *Metriopelia melanoptera*; *Leptotila cassini*, *verreauxi*, *rufaxilla*; *Geotrygon versicolor*, *montana*; *Staroenas cyanocephala*; *Goura cristata*; *Treron curvirostra*, *australis*, *calva*; *Ducula goliath*, *bicolor*.

The starch gel patterns of the Columbidae are all basically similar to one another and, as a group, they are readily distinguished from the patterns of other families. Within the Columbidae the patterns show certain variations in the mobilities and concentrations of the main components among the genera. The outstanding characteristic of the patterns is the tight elliptical banding displayed by the ovalbumins and ovomucoids. This distinguishes the patterns of pigeons from nearly all other groups of birds. The conalbumins are tightly bunched together as in the patterns of the Anseriformes and Galliformes. Component 18 differs in no substantial way from those of other groups. A prealbumin is present in many patterns just anodal to the ovalbumin. The patterns appear to lack minor bands between the major components.

Several genera share a pattern in which the conalbumin has a mobility of about 2.5 cm, an ovomucoid mobility of about 5.0 cm, and an ovalbumin mobility of 7.0 cm or less. They include *Zenaida*, *Columbina*, *Geotrygon*, *Staroenas*, *Claravis*, and *Metriopelia*. In these genera the ovomucoid is more concentrated than the ovalbumin.

The patterns of *Streptopelia* differ from this type in having conalbumins that move more rapidly toward the anode. The patterns of the New World species of *Columba* (e.g., *C. leucocephala*, *picazuro*) have slower conalbumins, and the ovalbumin and ovomucoid are closer together. In the Old World species of *Columba* the ovalbumin and ovomucoid are so close together that they are not resolved as distinct components except in dilute samples. *Leucosarcia* also has a single broad band at about 6.0 cm that probably represents both an ovomucoid and an ovalbumin. Apparently the same phenomenon occurs in the pattern of *Phaps chalcoptera*, except that a rather concentrated prealbumin is present at about 7.0 cm, and the conalbumins migrate at about 4.0 cm. These features give the pattern of *Phaps* a different appearance, but the shapes of the bands are clearly like those of other pigeons. *Petrophassa* differs from *Phaps* in its egg white pattern. In *Aplopelia* the pattern is like that of the group first described except that the conalbumins, ovomucoid and ovalbumin all have slower mobilities.

The patterns of *Ducula* and *Treron* are quite similar to one another. They differ from those of most other pigeons in having the ovalbumin and ovomucoid rather widely separated. A prealbumin is lacking.

Goura does not differ from other columbids in its pattern. It is, for example, similar to that of *Columba leucocephala* and *Oena capensis*.

Similarities to the columbid pattern are found only in the patterns of the Psittaciformes. The parrots *Aratinga mitrata* and *Psittacus erithacus* have elliptical ovalbumins and ovomucoids of about the same mobility as in some of the columbid patterns. The patterns of the parrots also show a prealbumin, but their conalbumins are indistinct and migrate between the origin and Component 18.

The patterns of the sandgrouse differ in nearly all aspects from those of the pigeons. The conalbumins migrate between the origin and Component 18. The ovomucoid and ovalbumin have a greater anodal mobility than those of the pigeons and lack the characteristic shape. In all respects the patterns of the sandgrouse are more similar to those of the shorebirds than they are to those of any other group. The patterns of the sandgrouse differ from those of the shorebirds only in having slightly faster ovalbumins and ovomucoids.

CONCLUSIONS

The sandgrouse may be most closely related to the shorebirds, but the conflicting interpretations of other characters make it important to obtain additional data from all sources before presenting an opinion on this question. The sandgrouse seem to have no obvious ties with the Galliformes.

The nearest relatives of the Columbidae may be the parrots, although they may be allied as well to the shorebirds. The connection to the shorebirds may be through the sandgrouse, but they could also represent a separate evolutionary trend.

Within the Columbidae a close relationship among the fruit pigeons (at least *Treron* and *Ducula*) seems to be indicated. Similarly there seems to be a closely allied group consisting of the ground doves of the New World, as well as *Zenaida*, *Metriopelia*, and possibly *Leptotila*. Obviously, any detailed consideration of relationships within the family using biochemical data must await the acquisition of material from many more genera.

ORDER PSITTACIFORMES

Family Psittacidae, Lories, Parrots, Macaws

Wetmore, 1960

INTRODUCTION

The parrots are readily defined by their distinctive, stout, hooked bills with prominent ceres, zygodactyl feet, and sparse, hard plumage. They are set well apart from other groups of birds and it may be true that "Die Papageien haben keine näheren Verwandten" (E. Stresemann, 1927-34: 824).

Because they seem to lack close relatives among living birds their nearest allies are difficult to determine and a considerable array of groups have been proposed. The strong, hooked bill suggests the raptorial birds and some systematists have placed the parrots with the hawks and owls. The zygodactyl foot is shared with the Piciformes and Cuculidae but the parrots and cuckoos have Type 1 flexor tendons while the piciforms have Gadow's Type 6. The parrots and cuckoos are also alike in having desmognathous palates, similar pelvic muscle formulas, holorrhinal, impervious nares, and in several other characters. They differ in bill structure, tarsal scutellation, presence (cuckoos) or absence (parrots) of the expansor secundariorum; eutaxic wing (cuckoos) or diastataxic (parrots); nestlings naked (cuckoos) or downy (parrots); caeca large (cuckoos) or caeca absent (parrots), and in several other characters.

The parrots and pigeons also share several characters but they differ in so many ways that a close relationship is difficult to support by using the traditional bases. However, as will be noted below, there is some evidence of a parrot-pigeon alliance and the suggestion must be given serious consideration in spite of their many differences.

The principal questions concerning the closest living relatives of the parrots thus seem to involve the Cuculiformes, Columbiformes and Piciformes. It seems highly unlikely that the birds of prey are actually involved in the problem but they should be considered if only because they have been mentioned as possible relatives.

The classification within the Psittaciformes is not the primary purpose of this study but we have included reviews of several classifications to indicate the diversity of opinion and the bases for it.

HISTORICAL REVIEW OF THE CLASSIFICATION

In a few of the early classifications that were based upon bill structure the parrots were associated with the birds of prey (e.g., Moehring, 1752; Bonaparte, 1853; Fitzinger, 1856-65) but in most systems they were placed with or close to the toucans, woodpeckers and cuckoos, indicating that the zygodactyl foot was the determining factor in their allocation (e.g., Linnaeus, 1758; Brisson, 1760; Illiger, 1811; Merrem, 1813; Vieillot, 1816; Temminck, 1820; Cabanis, 1847).

Nitzsch (1840) placed the parrots in his order of picarian birds between the Picinae (woodpeckers) and Lipoglossae (*Buceros*, *Upupa*, *Alcedo*). He found much variation among parrots in the feather tracts, number of rectrices, and other characteristics of their plumage. G. Gray (1844-1849) recognized the families Psittacidae, Cacatuidae, and Strigopidae for the parrots and placed them in his order Scansores along with the piciform and cuculiform birds. Similarly, Lilljeborg (1866) placed the Psittacidae in his order Zygodactyli.

In Huxley's (1867) opinion, the parrots constitute a sharply defined group of birds with distant affinities possibly to the Aetomorphae (diurnal and nocturnal birds of prey) and the Coccygomorphae (a varied assemblage consisting of some or all of the members of the Cuculiformes, Coliiformes, Coraciiformes, Trogoniformes, and Piciformes).

Finsch (1867) provided the first important monograph of the Psittacidae. He found the parrots most similar to the Rhamphastidae (toucans) and mentioned similarities to the cuckoos. On the basis of external characters and the structure of the tongue he divided the Psittacidae into five subfamilies.

The tongue of the kea (*Nestor*) was studied by Garrod (1872), who found that it was like that of the owl parrot (*Strigops*) and hence the kea is a "typical parrot" and not related to the trichoglossine parrots.

In Garrod's (1874a) system, based upon the oil gland, furcula, carotids and the pelvic musculature, the birds with an ambiens were assigned to the subclass Homalognatae, those lacking it to the Anomalognatae. Thus the cuckoos, parrots, and pigeons were placed with the homalognatous birds while the Piciformes were in the other subclass. The cuckoos and parrots were put in adjacent suborders in the order Galliformes.

Garrod (1874d) proposed a classification of the suborder Psittaci, which, as modified by Beddard (1898), is outlined as follows:

Family Palaeornithidae: two carotids, ambiens present, oil gland present

Subfamily Palaeornithinae

Subfamily Cacatuinae: orbital ring complete

Subfamily Stringopinae: furcula absent

Family Psittacidae: left carotid superficial

Div.a: ambiens present

Subfamily Arinae

Div.b: ambiens absent

Subfamily Pyrrhurinae

Subfamily Platycercinae: furcula absent

Subfamily Chrysotinae: oil gland absent

Garrod (1876f) examined the anatomy of several parrot genera and assigned *Dasyptilus* (= *Psittichas*) and *Deroptyus* to the Pyrrhurinae and *Polytelis*, *Chalcopsitta* and *Coriphilus* (= *Vini*) to the Palaeornithinae.

Forbes (1879) cited characters of pterylosis, the superficial left carotid, beak, nostrils, cere, skull, and pelvis as showing a relationship among *Lathamus*, *Psephotus*, and *Platycercus*. He did not believe that *Lathamus* is close to *Trichoglossus* and argued that "the abnormal tufted tongue, the retention of the furcula, and the sharp pointed wings may be regarded as adaptations to its tree- and flower-dwelling modes of life . . ." (p. 174). Forbes (1880a) reported on the pterylosis and anatomy of *Nasiterna* (= *Micropsitta*) and concluded that its closest allies are most likely *Cyclopsittacus* (= *Opopsitta*) and *Psittacella*. He also thought that it is related to the ground parrots (*Pezoporus*, *Geopsittacus*) and more distantly to *Agapornis* and *Psittinus*.

Of the Psittaci P. Sclater (1880: 403) commented, "The affinities of this ancient group to other orders appear to be somewhat remote, but their most natural position seems to be between the Picariae and the Accipitres." He followed Garrod's (1874d) division of the parrots into families.

The parrots are closely related to the birds of prey, according to Reichenow (1881). He divided the parrots into the following nine families: Stringopidae (*Strigops*, *Pezoporus*, *Geopsittacus*); Plissilophidae (cockatoos and *Nestor*); Platycercidae, Micropsittacidae, Trichoglossidae, Palaeornithidae, Psittacidae (*Psittacus*, *Coracopsis*); Conuridae (*Ara*, *Aratinga*, *Enicognathus*, *Pyrrhura*, *Brotogeris*, *Bolborhynchus*, *Forpus*); Pionidae (remaining South American genera and *Poicephalus*).

Kingsley (1885) placed his order Psittaci between the Accipitres and the Picariae, which included the cuckoos, goatsuckers, colies, rollers, etc. His classification of families and genera essentially followed Reichenow (1881).

Fürbringer (1888) recognized only a single family in the Psittaciformes and championed the idea that the pigeons are the nearest relatives of the parrots. He also believed that the parrots are more distantly allied to the Galliformes and to the Coracornithes, a large assemblage composed of the Cuculiformes, Coraciiformes, Coliiformes, Strigiformes, Caprimulgiformes, Trogoniformes, Apodiformes, Piciformes, and Passeriformes.

In 1889 Fürbringer presented evidence to show that the peculiarities of *Strigops* are correlated with its terrestrial way of life.

Seebohm (1890a) placed the Psittaci in his subclass Falconiformes next to the birds of prey. In 1895 he pointed to the diastataxic wing of parrots as precluding any alliance with the cuckoos and cited the pterylosis and the presence of a cere as indicative of relationship to the raptorial birds.

Goodchild (1886, 1891) found that parrots have an arrangement of secondary coverts similar to that of hawks and owls. This pattern of feathers is shared also by the herons and cormorants.

Mainly on the basis of external characters Salvadori (1891) arranged the parrots in six families as follows:

Nestoridae (*Nestor*)

Loriidae (*Chalcopsitta*, *Eos*, *Domicella*, *Phigys*, *Vini*, *Trichoglossus*, *Psitteuteles*, *Glossopsitta*, *Charmosyna*, *Oreopsittacus*)

Cyclopsittacidae (*Neopsittacus*, *Psittaculirostris*, *Opopsitta*)

Cacatuidae: Cacatuinae (*Probosciger*, *Calyptrorhynchus*, *Callocephalon*, *Cacatua*); Calopsittacinae (*Nymphicus*)

Psittacidae: Nasiterninae (*Micropsitta*); Conurinae (*Andorhynchus*, *Ara*, *Rhynchopsitta*, *Aratinga*, *Cyanoliseus*, *Ognorhynchus*, *Enicognathus*, *Micropsittace*, *Pyrrhura*, *Myiopsitta*, *Amoropsittaca*, *Psilopsiagon*, *Bolborhynchus*, *Forpus*, *Brotogeris*, *Nannopsittaca*); Pioninae (*Amazona*, *Graydidascalus*, *Pionus*, *Deroptyus*, *Pionopsitta*, *Gypopsitta*, *Touit*, *Pionites*, *Poicephalus*); Psittacinae (*Psittacus*, *Corac-*

copsis, Psittrichas); Palaeornithinae (*Lorius, Geoffroyus, Prioniturus, Tanygnathus, Psittacula, Polytelis, Aprosmictus, Alisterus, Prosopieia, Psittacella, Bolbopsittacus, Psittinus, Agapornis, Loriculus*); Platycercinae (*Platycercus, Purpuricephalus, Northiella, Psephotus, Neophema, Cyanorhamphus, Eunymphicus, Melopsittacus, Pezoporus, Geopsittacus*)

Strigopidae (*Strigops*)

Sharpe (1891) placed the Psittaciformes between the Coccoyges (cuckoos) and the Scansores (woodpeckers, toucans, barbets, honeyguides). In his opinion, "the Parrots, however, do not appear to have any very close allies. In the character of the nestling they are not in the least Accipitrine, and the development of their feathers is carried on in true Picarian fashion—that is to say, that the new feathers are enclosed in the sheath till they attain almost their normal length; and in this respect the Parrots resemble Kingfishers and other Picarian birds. The mode of nesting, too, is Picarian" (p. 65).

Gadow (1892) selected 40 characters "from various organic systems" and used them in comparisons among avian groups. He used the parrots as an example of his method "of sifting characters" and found that the "Psittaci agree with Coccoyges in 31 points, with Pici in about 29, with Coraciidae 25, Falconidae 25, Striges 22, Bucerotidae 22, Gallidae 21 . . ." (p. 231). He concluded that "the Psittaci are much more nearly allied to the Coccoyges than to the Falconidae, and of the Coccoyges the Musophagidae are nearer than the Cuculidae because of the vegetable food, ventral pterylosis, presence of aftershaft, tufted oil-gland, absence of vomer, truncated mandible, and absence of caeca" (p. 232). His comparison between parrots and owls convinced him that these two groups are "far from each other" and that "the resemblances between the Pici and Psittaci have . . . to be looked upon as convergent analogies" (p. 234).

In his "Final Conclusion" (1892: 234–35) Gadow stated that the parrots and cuckoos share a common ancestor, with

the Psittacine twig to stand between that of the Musophagidae and looking towards the branch of the Striges, which again come out of the bigger branch of the Coraciiformes. This big branch and that of the Cuculiformes would ultimately combine into a still bigger branch; below this bifurcation would come off *Opisthocomus* and lower still that of the Gallidae. Thus the Psittaci permit us a glimpse at a large part of the Avine tree, namely at that big branch which downwards points towards the Galliformes and towards the Gallo-Ralline and Rallo-Limicoline region of the tree, while the same branch upwards ends not only in all the so-called Picariae but also in the Pico-Passeres.

In his classification (1892: 248–249) Gadow put this graphic dendrogram into a linear sequence as follows:

- Order Cuculiformes
 - Suborder Coccoyges: Cuculidae, Musophagidae
 - Suborder Psittaci: Psittacidae
- Order Coraciiformes
 - Suborder Striges
 - Suborder Macrochires
 - Suborder Colii
 - Suborder Trogones
 - Suborder Coraciae

Gadow (1893) divided the parrots into two families, Trichoglossidae and Psittacidae,

on the basis of the presence or absence of horny fibers on the tongue, the condition of the orbital ring, and the direction of the grooves on the maxilla. He also modified the sequence of the groups in his classification by moving the Coraciae to a position above the Striges (p. 301).

Beddard and Parsons (1893) found two main types of syringeal structure among a number of genera of parrots. In one group the semirings of the bronchi are straight but weak and cartilaginous and separated from each other by a membrane. *Cacatua*, *Probosciger*, *Calyptorhynchus*, and *Strigops* are similar in this respect. In another group the bronchial semirings are concave upwards and ossified, frequently being fused together. The genera sharing this condition include *Amazona*, *Prosopieia*, *Trichoglossus*, *Lorius*, *Pionus*, *Psittacus*, *Tanygnathus*, *Eos*, *Polytelis*, *Platycercus*, and *Poicephalus*. From the syringeal structure and the myology of the wing it was clear to these writers that *Strigops* is closely related to *Nestor* and *Calyptorhynchus*. They pointed out that the unusual structural features of *Strigops* are due to its terrestrial habits. Beddard and Parsons also thought that the Australian cockatoos are closely allied and suggested that the macaws (*Ara*) may be related to them.

Mivart (1895) described the hyoid osteology of *Psittacus*, *Lorius* (= *Domicella*), *Eos*, *Trichoglossus*, and *Strigops*. The three genera of lories had similar hyoids, but *Psittacus* differs from them in this character. Mivart found that the hyoid of *Strigops* was unlike those of the others, and he was unable to suggest its nearest relatives. Mivart (1896a) also examined the hyoids of *Nestor* and *Nanodes* (= *Lathamus*) and found resemblances between the former genus and the lories. The hyoid of *Lathamus* differed from those of the other genera studied. Mivart (1896b) also published a monograph of the Loriidae.

Beddard (1898a) reviewed the characters of the parrots and the classifications proposed by Garrod, Gadow, Fürbringer and others. He apparently approved of Garrod's (1874d) arrangement in general for he presented it completely (p. 269-70). Beddard noted (p. 271) that "the determination of the affinities of the parrots to other groups of birds is one of the hardest problems in ornithology." He commented on the proposals that the parrots might be related to falconiforms or galliforms and then stated (p. 271-72):

. . . The parrots, like the cuckoos, are a group of birds which are on the borderland between the Anomalognatae and the higher birds. . . . They show resemblances to the Passeres [in] the complicated musculature of the syrinx, the absence of biceps slip and expansor secundariorum, the presence of a cucullaris propatagialis, found in the Passeres and in the somewhat passeriform *Upupa* and *Pici*, the small number of cervical vertebrae, the total want of caeca, allying them not certainly to the Passeres but again to the *Pici* and many Anomalognatae, the reduced clavicles of some genera. Zygodactyle feet, moreover, are not found among the higher birds except in the Cuculi and the Musophagi, which are, similarly to the parrots, on the border line between the Anomalognatae and higher birds.

Beddard also noted that in the Anomalognatae a catapophysial canal is found only in the *Pici*, passerines and one species of parrot. He concluded with the rather vague opinion that the parrots "have emerged from a low anomalognatous stock at a time not far removed from that at which the Cuculi and Musophagi also emerged, but that there is not a common starting point of the three groups" (p. 272).

Thompson (1899) criticized Garrod's (1874d) classification of the parrots, pointing out that Garrod's use of a few unsatisfactory characters led him to propose an unnatural arrangement. Thompson examined the orbital ring, structure of the hyoid,

osteology of the tympanic region, and morphology of the quadrate. From these data he suggested that *Nestor* and *Strigops* belong in separate, monotypic families. He found many similarities among the Australian genera *Platycercus*, *Lathamus*, *Neophema*, *Psephotus*, and *Nymphicus*. In his opinion, *Melopsittacus* belongs to this group. Closely allied to these are *Polytelis*, *Aprosmictus*, and *Prosopieia*. Not far from the platycercine group are *Lorius*, *Trichoglossus*, *Eos*, and *Glossopsitta*. Although Thompson postulated interrelationships among many other parrot genera, he did not propose a formal classification of the group and did not speculate upon their nearest relatives.

According to H. Clark (1901b), the parrots and the birds of prey (hawks, vultures, owls) have a "falconiform" type of pterylosis. The pigeons and sandgrouse are "columbiform" and the cuckoos "passeriform" in their pterylosis.

Mitchell (1901a) found little variation in the configurations of the intestinal tracts in 10 genera of parrots. He was uncertain of the affinities of parrots but thought that the type of arrangement of the gut could best be derived from a coraciiform type. Beddard (1910) examined the intestinal tracts of additional parrots but was also unable to conclude anything about the affinities of the group.

Shufeldt (1902b) reviewed his earlier paper (1886) on "*Conurus*" (= *Conuroopsis*) and added some data on *Strigops*. He compared *Conuroopsis* with *Ara*, *Cacatua* and *Calyptorhynchus* and suggested that the parrots may be related to the owls but was skeptical about a relationship to the falconiforms. He recommended a separate family for *Strigops* because of the reduced forelimb and carina.

Mudge (1902) proposed a classification of the parrots based on the musculature of the tongue and osteology of the hyoid. A summary of his system follows:

Family Loriidae: Eosinae (*Eos*), Loriinae (*Lorius*, *Vini*)

Family Nestoridae: (*Nestor*)

Family Psittacidae

"Group 1": Psittaculinae (*Forpus*, *Cyanorhamphus*, *Eunymphicus*, *Prosopieia*, *Pionites*); Pyrrhurinae (*Loriculus*, *Pyrrhura*)

"Group 2": Bolborhynchinae (*Pezoporus*, *Platycercus*, *Bolborhynchus*, *Prioniturus*); Tanygnathinae (*Poicephalus*, *Tanygnathus*, *Aprosmictus*, *Pionopsitta*, *Psittinus*); Conurinae (*Psephotus*, *Conurus*, *Psittacula*, *Brotogeris*); Psittacinae (*Derophtus*, *Psittacus*); Eclectinae (*Lorius*, *Coracopsis*); Chrysotinae (*Cyanoliseus*, *Amazona*, *Ara*); Cacatuinae (*Cacatua*, *Strigops*, *Probosciger*, *Nymphicus*, *Micropsitta*, *Calyptorhynchus*).

Chandler (1916), from his study of feather structure, believed that the parrots and cuckoos are closely related and that they should be included in the same order. He also thought that the parrots are allied to the Coraciiformes *sensu lato*, including Striges, Caprimulgi, Trogones, Cypseli, and Pici.

The skeleton of the kea (*Nestor notabilis*) of New Zealand was described by Shufeldt (1918b) who concluded that a family Nestoridae was to "be considered an established fact" (p. 42) because of its distinctive morphology.

E. Stresemann (1927-34) was unable to suggest any group as the nearest ally of the parrots.

For the parrots Peters (1937) recognized only a single family, but he erected his subfamilies upon the families of Salvadori (1891). Peters' subfamilies included the Strigopinae (*Strigops*), Nestorinae (*Nestor*), Loriinae (lories of Australia, New Guinea, etc.), Micropsittinae (*Micropsitta*), Kakatoeinae (cockatoos), and Psittacinae (the remaining genera).

Von Boetticher (1943b) made several suggestions regarding the allocation of some parrot genera and in 1964 he developed the following classification for the

Psittacidae: subfamilies Nestorinae, Psittichasinae, Kakatoeinae, Micropsittinae, Trichoglossinae (tribes Psittaculirostrini, Trichoglossini), Strigopinae, Psittacinae (Platycercini, Loriini, Loriculini, Psittacini, Araini). In his monograph of the parrots Kuroda (1967) followed von Boetticher's system.

The nearest allies of the parrots were unclear to Mayr and Amadon (1951), who regarded them as a "strongly differentiated group." In their opinion, "resemblance to the Accipitres is probably mere convergence, and relationship to the Cuculi, championed by Gadow, must be rather distant at best. McDowell has found similarities between the humeri of parrots and those of pigeons" (p. 9).

Glenny studied the variation in the carotid arteries (1951, 1957) and the clavicles (1959) of parrots and in 1957 he proposed a classification of the Psittacidae based on the variation in the carotid configurations. His arrangement of subfamilies is summarized as follows: Strigopinae, Loriinae, Micropsittinae, Psittacinae (*Melopsittacus*, *Loriculus*, *Neophema*, *Agapornis*, *Alisterus*, *Polytelis*, *Psittacula*, *Tanygnathus*, *Lorius*, *Prioniturus*), Kakatoeinae, Nestorinae, Lathaminae, Palaeopsittacinae (*Cyanorhamphus*, *Northiella*, *Platycercus*, *Psephotus*, *Prosopieia*, *Psittichas*, *Coracopsis*, *Psittacus*, *Poicephalus*), Neopsittacinae (all Neotropical genera).

Verheyen (1956f) found osteological similarities among the Psittaciformes, Columbiformes, and Cuculiformes. He recognized five families of parrots, with their constituent subfamilies as follows: Strigopidae, Kakatoeidae, Psittacidae (Amazoninae, Arinae, Psittaculinae, Psittacinae), Platycercidae (Nymphicinae, Nestorinae, Polytelinae, Platycercinae, Lathaminae), Trichoglossidae (Trichoglossinae, Loriculinae, Micropsittinae). In his 1961 classification Verheyen placed the Psittaciformes between the Columbiformes and Coraciiformes and mentioned that they seem to have a distant relationship to the Falconiformes and Cuculiformes.

Sibley (1960) examined the egg white proteins of 10 species of parrots using paper electrophoresis. The patterns of the six genera were quite different from one another and Sibley suggested that this diversity might indicate that large genetic gaps have evolved between the various groups of parrots although they have retained the similar parrot type of beak, foot and feather structure. That closely related parrots do have similar egg white proteins was indicated by the common pattern found in five species of *Agapornis*.

Mainardi (1962b) also found unusual diversity within the Psittaciformes in his study of red-cell antigens, and Gysels (1964b) reported a high degree of heterogeneity in the eye lens and muscle proteins of parrots. Gysels also noted that the mobilities of the "typical song bird component" and of the muscle protein "myogen" in the parrot *Agapornis* were the same as those in *Falco* and differed from those of other parrots. He suggested that his results might reopen the question of a relationship between parrots and the birds of prey.

Brereton and Immelmann (1962) examined head-scratching behavior among parrots and on this criterion found that the subfamilies Strigopinae, Nestorinae, Loriinae, and Kakatoeinae were distinct groups. The Psittacinae, however, seemed to be heterogeneous. Brereton (1963) proposed a classification of the Psittaciformes based on 12 characters in addition to the method of head scratching. These characters included the development of the temporal and postsquamosal fossae; presence or absence of the ambiens muscle, furcula, and oil gland; arrangement of carotid arteries; wing shape; morphology of the hyoid; shape of the auditory meatus; degree of ossification of the orbital ring; tail length; and geographic distribution. A summary of Brereton's classification follows:

Superfamily Cacatuoidea

Cacatuidae (*Strigops*, *Probosciger*, *Calyptorhynchus*, *Callocephalon*, *Cacatua*);
Palaeornithidae (*Tanygnathus*, *Lorius*, *Prioniturus*, *Geoffroyus*, *Psittacula*, *Psit-*

tinus); Amazonidae (*Anodorhynchus*, *Ara*, *Aratinga*, *Pionites*, *Pyrrhura*, *Pionopsitta*, *Deroptyus*, *Amazona*, *Brotogeris*, *Pionus*); Psittacidae (*Poicephalus*, *Psittacus*, *Coracopsis*, *Psittichas*, *Prosopaea*)

Superfamily Platycercoidea

Nestoridae (*Nestor*); Loriidae (*Trichoglossus*, *Vini*, *Chalcopsitta*, *Eos*, *Domicella*, *Glossopsitta*); Micropsittidae (*Loriculus*, *Micropsitta*, *Agapornis*); Alisteridae (*Alisterus*, *Aprosmictus*, *Polytelis*, *Nymphicus*); Pezoporidae (*Melopsittacus*, *Geopsittacus*, *Pezoporus*); Platycercidae (*Neophema*, *Platycercus*, *Lathamus*, *Eunymphicus*, *Cyanorhamphus*, *Barnardius*, *Purpuricephalus*); Forpidae (*Forpus*, *Amoropsittaca*, *Psilopsiagon*, *Bolborhynchus*).

Forshaw (1969), in his book on Australian parrots, recognized the families Loriidae, Cacatuidae, and Psittacidae.

SUMMARY

As championed by Gadow, the Cuculidae have been most often suggested as the nearest relatives of the parrots. Other groups that have been proposed as allies of the parrots include the Piciformes, Columbiformes, Falconiformes, Strigiformes, and Coraciiformes. The consensus is that the similarities between parrots and the birds of prey are due to convergence. No convincing body of data exists to support an alliance between the parrots and any of the other groups. The proposals to unite the parrots with either the Cuculiformes or Piciformes seem to have been influenced primarily by the possession of zygodactyl feet, although other characters can be cited in support of either proposal.

On the arrangement of groups within the Psittaciformes there is little agreement. Some groups, such as the cockatoos, seem to be natural, but their nearest relatives among the parrots are obscure. The parrots have had a complex evolutionary history, and their interrelationships need further study.

THE EGG WHITE PROTEIN EVIDENCE

ORDER PSITTACIFORMES

FAMILY PSITTACIDAE, Parrots, Lories, Macaws, Cockatoos. 36/316, figs. 29, 30.

Species examined (nomenclature follows Peters, 1937, except for the use of *Cacatua*, which follows Mayr, Keast, and Serventy, 1964): *Calyptorhynchus funereus*, *baudinii*, *magnificus*; *Cacatua galerita*, *sanguinea*, *tenuirostris*, *roseicapilla*; *Nymphicus hollandicus*; *Aratinga mitrata*, *canicularis*; *Myiopsitta monachus*; *Amazona viridigenalis*, *autumnalis*, *ochrocephala*; *Psittacus erithacus*; *Lorius roratus*; *Psittacula columboides*; *Polytelis anthopeplus*, *alexandrae*; *Alisterus scapularis*; *Psittinus cyanurus*; *Agapornis roseicollis*, *fischeri*; *Platycercus elegans*, *caledonicus*, *eximius*, *icterotis*, *zonarius*; *Psephotus haematonotus*, *varius*; *Neophema elegans*, *petrophila*, *bourkii*, *chrysostoma*; *Cyanorhamphus novaezeelandiae*; *Melopsittacus undulatus*.

The egg white protein patterns of the parrots make up several groups that have basic features in common. One group of patterns includes those of *Cacatua*, *Calyptorhynchus*, *Nymphicus*, *Cyanorhamphus*, *Psittacus*, and *Aratinga*. In this pattern type Component 18 migrates about 1.0 cm from the origin. Anodal to it are the conal-

bumins, which are not sharply defined. The ovomucoid migrates anodally between 5.0 and 6.0 cm. It is not subdivided. In the ovalbumin region there is a broad band anodal to which are two crescent-shaped bands. These bands are sharply defined in the patterns of *Aratinga* and *Cyanorhamphus*, less so in the patterns of *Cacatua* and *Calyptorhynchus*. It is not known if these bands are prealbumins or additional components of the ovalbumin. In these patterns the ovomucoid occupies an area equal to or larger than that covered by the ovalbumin, but the two proteins stain with the same density.

A second group includes the patterns of *Polytelis* and *Alisterus*, which differ in having a slower ovomucoid; hence, the ovalbumins and ovomucoid are more widely separated. The double ovalbumin is seen as an area in which the halves stain with differing intensities. Some of the conalbumins migrate between the origin and Component 18; others move cathodally.

A third pattern type is shared by the genera *Platycercus*, *Psephotus*, and *Neophema*. In these genera the ovalbumin and ovomucoid have slower mobilities than those of other parrots. The ovalbumin is double, and it stains less intensely than the ovomucoid. The ovomucoid is single in *Platycercus* and *Psephotus* but subdivided in *Neophema*. The conalbumins migrate to both sides of Component 18.

A fourth variation is represented by the patterns of *Agapornis*, *Psittinus*, and *Melopsittacus*. The conalbumins are indistinct and migrate anodal to Component 18. The ovomucoid migrates only to about 4.0 cm. It is a broad, dense region that is subdivided into a number of small bands. The ovalbumin is also a broad band anodal to which is a well-defined, crescent-shaped component, which may be a prealbumin.

The patterns of the parrots thus show considerable variation superimposed upon a common pattern type. Resemblances exist among the patterns of parrots and those of pigeons. The two groups share a characteristic elliptical shape of the ovomucoid and ovalbumin. They are the only two groups in which the ovomucoid often is larger and more densely staining than the ovalbumin. This character is prominent in the parrot genera *Platycercus*, *Neophema*, and *Psephotus*, and in the pigeons *Zenaida*, *Columbina*, *Geotrygon*, and others. The patterns of the Psittacidae are unlike those of the Columbidae in that they lack the dense cluster of conalbumins.

The patterns of the parrots are unlike those of the Cuculiformes in most ways; neither are there any striking similarities in their patterns to those of the Piciformes, Coraciiformes or Strigiformes.

CONCLUSIONS

Although the parrots are a distinctive group of birds, their nearest allies seem to be the pigeons. This view is supported by the egg white proteins and some anatomical evidence. We propose that the Psittaciformes and Columbiformes be united in a single superorder.

Within the Psittacidae the similarities among the cockatoos and among most of the platycercine parrots are not surprising, since there is a body of evidence suggesting that these groups are closely related. Some of the other genera, however, which share similar egg white patterns differ in the characters which have been used in classifying the Psittacidae. Pending the employment of additional techniques and the acquisition of material from many more genera, we decline to draw any conclusions on relationships within the order.

ORDER CUCULIFORMES

Suborder Musophagi

Family Musophagidae, Turacos

Suborder Cuculi

Family Cuculidae

Wetmore, 1960

Subfamily Cuculinae, Cuckoos, Roadrunners

Subfamily Crotophaginae, Anis, Guira Cuckoos, Hoatzins

Sibley and Ahlquist, present work

A. CUCULIFORMES EXCEPT *OPISTHOCOMUS*

INTRODUCTION

The Cuculiformes are one of the most diverse orders and various authors have expressed doubt as to whether or not the Musophagi and Cuculi are related closely enough to be placed in the same order. One of the principal reasons for associating the two groups is that both have a zygodactyl foot in which the flexor tendons are of Gadow's "Type 1." However, in the Musophagi the foot is only "semi-zygodactyle" (Moreau, 1938), for the fourth toe is not permanently directed backwards. Actually, the parrots have a foot structure more like that of the Cuculinae than do the Musophagi. Table 3 lists some of the differences between the turacos and the cuckoos.

The relationships of the hoatzin (*Opisthocomus*) will be discussed in a separate section below. We believe that *Opisthocomus* is a member of the Cuculi, rather than the Musophagi, and thus the supposed link between the Cuculiformes and Galliformes is destroyed.

There is an extensive literature on social or brood parasitism in cuckoos but most of the papers contain nothing pertinent to the problems of ordinal and familial relationships. Some, e.g., Friedmann's papers on *Clamator* (1964) and *Chrysococcyx* (1968), discuss systematic relationships within the Cuculidae. The existence of brood parasitism is itself not a substantial basis for speculation about higher category relationships, according to Berger (1960: 82), who found that morphological characters and the presence or absence of brood parasitism were not highly correlated. Similarly,

TABLE 3. Differences between the Cuculidae and Musophagidae

Cuculidae	Musophagidae
Pelvic muscles: AFGXY+, ABFGXY+, ABEFGXY+	Pelvic muscles: ABDFGXY+V
Expansor secundariorum "cuculine"	Expansor secundariorum "ciconiine"
2 bony canals in hypotarsus	1 bony canal in hypotarsus
17 or 18 presynsacral vertebrae; 4 dorsal vertebrae typical	19 presynsacral vertebrae; 5 dorsal vertebrae typical
Perforated atlas	Notched atlas
Typical furcula present	Furcula absent
No bony canal formed by coracoid	Bony canal formed by dorsal processes of coracoid
Lacrimal bone "cuculine"	Lacrimal bone "musophagine"
Oil gland nude	Oil gland tufted
Aftershaft absent or vestigial	Aftershaft present
Eyelashes present	Eyelashes absent
Pattern of dorsal feather tracts variable, but unlike Musophagidae	Dorsal feather tracts unlike Cuculidae
Foot zygodactyl: fourth toe permanently reversed	Foot semi-zygodactyl: fourth toe held at right angles to main axis of foot.
Uncinate bone in skull only in <i>Scythrops</i> and <i>Piaya</i>	Uncinate bone in skull
Small vomer present	Vomer absent
Caeca present	Caeca absent
4 ribs reach sternum	5 ribs reach sternum
Main leg artery the ischiatic (except in <i>Centropus</i>)	Main leg artery the femoralis
Pigment turacin absent	Turacin present
14 cervical vertebrae	15 cervical vertebrae
Coracoids separate	Coracoids overlapping

SOURCES: Gadow, 1892; Berger, 1960: table 4; Moreau, 1938.

Friedmann (1964: 10) noted that breeding habits are less reliable indices of relationship than are morphological characters.

The principal questions concerning the relationships of the Cuculiformes are:

- 1) Are the Cuculi closest to the Musophagi, *Opisthocomus*, the Psittaciformes, the Caprimulgiformes, the Coliiformes, or some other group?
- 2) Are the Musophagi closest to *Opisthocomus*, the Cuculi, the Galliformes, the Psittaciformes, or some other group?

HISTORICAL REVIEW OF THE CLASSIFICATION

The cuckoos have long been associated with the same groups currently considered to be their closest relatives. For example, Merrem (1813) included *Cuculus*, *Trogon*, *Bucco* and *Crotophaga* in his Cocyges and nearby, in the Levirostres, were *Ramphastos*, *Scythrops* and *Psittacus*. Nitzsch (1840) set up an order Picariae, which included the cuckoos, swifts, woodpeckers, parrots, turacos, *Colius*, *Opisthocomus*, goatsuckers, *Todus*, *Buceros*, *Upupa* and *Alcedo*. Within the picarian birds one of the main divisions was the Cuculinae, including *Cuculus*, *Coccyzus*, *Saurothera*, *Crotophaga*, *Scythrops*, *Phaenicophaeus*, *Leptosomus*, *Indicator*, and *Trogon*. Nitzsch admitted, however, that "this group . . . has no definite pterylographic character; the only character that appears to occur in all of them is the nakedness of the tip of the oil-gland, which is not furnished with a cirlet of feathers" (p. 90, Sclater's translation). Citing the presence of an aftershaft, ten rectrices, and the tufted uropygial gland, he placed the turacos in his Amphibolae, which included *Opisthocomus* and *Colius*.

G. Gray (1844-49) put the Musophagidae among the passerine birds near *Colius*, *Opisthocomus*, and the Bucerotidae. He included the Cuculidae in his order Scansores, which contained all birds with zygodactyl feet. Lilljeborg (1866) also defined an order Zygodactyli. In addition to psittaciform and piciform birds this order contained the Musophagidae (including *Colius*) and the Cuculidae (including *Indicator*).

In Huxley's classification (1867, 1868b) based on palatal characters the Coccymorphae include four groups: a) Coliidae; b) Musophagidae, Cuculidae, Buceronidae, Ramphastidae, Capitonidae, Galbulidae; c) Alcedinidae, Bucerotidae, Upupidae, Meropidae, Momotidae, Coraciidae, and d) Trogonidae. The Psittacomorphae, containing only the parrots, and the Heteromorphae, containing only the hoatzin (*Opisthocomus*), were adjacent to the Coccymorphae.

Thus, the tradition for the association of these several groups was established more than a century ago.

Garrod (1873d, 1874a) divided the Aves into those with an ambiens muscle (Homalagonatae) and those lacking it (Anomalagonatae). Among the Homalagonatae were the Musophagidae and Cuculidae and next to them were the Psittaci. The gallinaceous birds also were nearby. The Anomalagonatae included all of the other groups mentioned above in Huxley's classification. Garrod's system was obviously unnatural and was never accepted (Newton, 1893-96: Intro., 92).

P. Sclater (1880) disagreed with Garrod's allocation of the cuculiform birds. He admitted that they show "much affinity" with the galliforms but believed that they belong among the picarian birds of Nitzsch. He placed the Cuculidae and Musophagidae in a suborder Cocyges in his large order Picariae. The order Scansores of Reichenow (1882) included the piciform birds, Coliidae, Musophagidae, Crotophagidae, and Cuculidae. Stejneger (1885) set up an order Picariae, roughly equivalent

to that of Nitzsch, and included a superfamily Cuculoideae for the Cuculidae and Musophagidae.

The structural characters of the cuckoos were reviewed by Beddard (1885), who proposed a classification of the Cuculidae into three subfamilies: Cuculinae, Phoenicophaginae and Centropodinae.

Shufeldt (1885a; 1886a-c) published several papers on the anatomy of the roadrunner (*Geococcyx*) and reviewed the characters of the cuckoos. He proposed that the North American Cuculidae should be placed in three subfamilies: Crotophaginae (*Crotophaga*), Centropodinae (*Geococcyx*) and Cuculinae (*Coccyzus*). Shufeldt considered it possible that *Geococcyx* might be related to such birds as *Dacelo gigas* (Alcedinidae) or the Galbulidae.

A monograph of the Musophagidae by Schalow (1886) reviewed the systematic treatments of the group by earlier authors (p. 4-6). He noted that the turacos were placed with the cuckoos in some of the earliest classifications but that many other groups have also been proposed as allies, including the pigeons, galliforms, woodpeckers, trogons, puffbirds, parrots, colies, rollers, *Opisthocomus* and even certain passerines. In Schalow's opinion (p. 6), the musophagid genera *Schizorhis* (= *Crinifer*) and *Gymnoschizorhis* (= *Crinifer*) indicated a relationship to the Coliidae.

Fürbringer (1888) combined the Cuculidae and Musophagidae in a suborder, the Coccygiformes, and considered them to be an outlying group of his order Coracornithes. In his opinion, their nearest relatives are the Galbulidae and Bucconidae, which link the cuculiform birds to the Pico-Passeres.

Seebohm (1890a) placed his order Coccyges, including the Cuculi and Musophagi, near the orders Columbae and Pico-Passeres. In 1895 Seebohm defined an order Cuculiformes on the basis of the deep plantar tendons, presence of the fifth secondary, desmognathous palate, altricial young, and the arrangement of the spinal pteryla. This order, containing the suborders Cuculi (Cuculidae and Musophagidae) and Upupae, was part of his subclass Aegithomorphae, which included the Passeriformes, Turniciformes, and Galliformes.

Goodchild (1891) studied the arrangement of the secondary coverts of the cuculiform birds. In his opinion, "the normal cuckoos . . . are intermediate between the Picarian birds and the Pigeons, while the Ground Cuckoos approach the Peristeropods [Cracidae, Megapodiidae] and the Gouridae" (p. 327).

Within an order Picariae, Shelley (1891) recognized the suborder Coccyges for the Cuculidae and Musophagidae. He divided the cuckoos into six subfamilies with their constituent genera as follows:

Cuculinae (*Clamator*, *Pachycoccyx*, *Caliechthrus*, *Cuculus*, *Cercococcyx*, *Cacomantis*, *Misocalius*, *Chrysococcyx*, *Chalcites*, *Coccyzus*, *Urodynamis*, *Eudynamis*, *Microdynamis*, *Rhamphomantis*, *Scythrops*)

Centropodinae (*Centropus*)

Phoenicophaginae (*Saurothera*, *Piaya*, *Zanclotomus*, *Taccocua*, *Rhopodytes*, *Rhinortha*, *Phaenicophaeus*, *Rhamphococcyx*, *Ceuthmochares*, *Dasylophus*, *Lepidogrammus*, *Coua*)

Neomorphinae (*Carpococcyx*, *Neomorphus*, *Geococcyx*, *Morococcyx*)

Diplopterinae (*Tapera*, *Dromococcyx*)

Crotophaginae (*Crotophaga*, *Guira*)

In 1891 Sharpe included the Cuculi and Musophagi in his Cuculiformes, commenting that "these birds, . . . though zygodactyle, possess other characters which seem to show that at the present day, at least, they have little to do with the so-called Picariae, and in many respects exhibit Galline affinities" (p. 65). In his diagram of

relationships (plate 9) the Cuculi and Musophagi appear approximately equidistant from the Columbæ and Colii. In his linear list (plate 10) they occur between the Psittaci and Trogones.

Gadow (1892) found that the parrots (Psittaci) agree with the cuckoos (Coccyges) in 31 of his 40 characters and that (p. 231) "the Coccyges and Gallidæ are intimately connected with each other through *Opisthocomus*." The Psittaci were found to agree with the Pici in 29 points, with the Coraciidæ and Falconidæ in 25 and with the owls in 22. He concluded (p. 232): "The Psittaci are much more nearly allied to the Coccyges than to the Falconidæ, and of the Coccyges the Musophagidæ are nearer than the Cuculidæ. . . ." The Cuculiformes were also linked to the Coraciiformes and, in a "Final Conclusion," Gadow recorded his belief in a "close affinity between the Psittaci and Coraciidæ, but less intimate than with the Coccyges . . . [which] are, however, closely related to the Coraciidæ, and are (as indicated by the *Opisthocomus*-Gallidæ connexion) the lowest of the three groups of Psittaci, Coraciidæ, and Coccyges" (p. 234-35). Gadow placed the cuckoos (including the Musophagidæ) and the parrots in his order Cuculiformes, next to his Coraciiformes, which included the owls, nightjars, swifts, hummingbirds, colies, trogons, rollers, motmots, kingfishers, bee-eaters, hoopoes, hornbills, and wood-hoopoes.

The Cuculi and Musophagi were treated as separate, but adjacent, groups by Beddard (1898a). However, he tabulated several differences between them and noted (p. 284) that "the skull of *Corythaix* is barely desmognathous, and by no . . . means especially like that of a cuckoo. . . ." Beddard thought that the cuckoos show similarities to the "Pico-Passeres . . . in the structure of the foot, . . . the tendons of the patagium, . . . the marked resemblance in the syrinx to . . . Caprimulgi, and in a less degree to the Striges" (p. 281). Beddard also investigated the anatomy of *Scythrops* (1898b), of *Carpococcyx* (1901a) and of *Hierococcyx* and allied genera (1902b).

The intestinal coiling pattern of the Cuculi is derived from a "coraciiform-cuculiform metacentre," according to Mitchell (1901a). He found that a similar pattern is shared by *Cacomantis*, *Carpococcyx*, *Centropus*, *Crotophaga*, *Guira*, and *Scythrops* but ascribed the differences in the intestinal tract of the Musophagi to their frugivorous diet.

Shufeldt (1901g) reviewed the osteology of the cuckoos, concluding that their closest affinities were with "the Musophagidæ, Bucconidæ, Galbulidæ, Meropidæ, Momotidæ, Bucerotidæ, Upupidæ, Todidæ, Coraciidæ, Rhamphastidæ, Capitonidæ and perhaps some few others" (p. 47). He considered that the cuckoos must be "quite remote" from "the Caprimulgi, the Cypseli, the Trogones, the Trochili and the Pici. . . ." He declined to follow Garrod in placing "the Cuculidæ and Musophagidæ together in with the Gallinaceous birds!" (p. 48). Shufeldt (1904b) recognized the Cuculi and Musophagi as suborders within an order Cuculiformes. In a later paper (1909), on the osteology of *Clamator glandarius*, he found no reason to change his previous classification.

Pycraft's (1903c) studies of the skeleton of the Cuculiformes led him to conclude that the cuckoos and turacos are osteologically similar. He thought that the skull characters indicate a relationship between cuckoos and some Coraciidæ and Bucconidæ and through the Musophagidæ to *Opisthocomus*.

His studies of feather structure convinced Chandler (1916) that the cuckoos and parrots are "undoubtedly related," and he followed Knowlton (1909) in placing them in one order. Regarding other relationships Chandler (p. 367) believed that

the Cuculiformes are very closely related to the Coraciiformes, and should probably be considered as nearly allied to the immediate forerunners of this group. The question of their descent is likewise easy, the only lower groups to which they

show affinity being the peristeropode Galli and the Columbidae; in general form of pennaceous barbules they are nearer to the former, but in the structure of the down and in some details of the structure of the pennaceous barbules, e.g., the prongs on the hooklets, they show affiliation to the latter. The Cuculidae, especially the Musophagidae, come nearer the gallinaceous and columbid birds, while the parrots are nearer the Coraciiformes in the structure of their feathers.

E. Stresemann (1927-34) placed the cuckoos and turacos together in the order Cuculidae. He considered *Opisthocomus* to be closely allied to the Galliformes and to resemble the Musophagidae only by convergence (p. 818). However, he (1965) changed his mind about the relationship between *Opisthocomus* and the Galliformes when he discovered important differences in their molt patterns.

Moreau (1938) described the growth, behavior and other aspects of the biology of *Turacus* (= *Tauraco*) *fischeri*. He also considered the question of the "semi-zygodactyly" of the musophagid foot and concluded that the condition in the turacos can be described "as having a fourth (outside) toe that can be brought back to form an angle of about seventy degrees with the first toe, and forward until it almost touches the third toe, but normally is held at right angles to the main axis of the foot" (p. 668-69). This condition thus differs from that of the truly zygodactyl foot of the Cuculidae, in which the fourth toe is permanently reversed.

The genus *Coua*, a group of 10 species of non-parasitic cuckoos endemic to Madagascar, has been studied by Rand (1936), Milon (1952) and Appert (1970). *Coua* is given subfamily rank (Couinae) by some authors (e.g., Thomson, 1964) and included in the Centropodinae by others. Superficially the couas resemble *Centropus* and the turacos (Musophagidae) (Moreau, 1964).

Peters' (1940) classification of the Cuculidae was much like that by Shelley (1891). Peters transferred *Tapera* and *Morococcyx* to the Neomorphae and erected a separate subfamily for *Coua*.

Lowe (1943) found such large differences between the Cuculidae and the Musophagidae in pterylosis, osteology, and myology that he recommended their placement in separate orders. He also contrasted their coloration, color patterns and food habits.

The Mallophaga of the Musophagidae are more like those of the Galliformes than those of the Cuculidae, according to Clay (1947). She also discovered that the Mallophaga of *Opisthocomus* show no obvious relationships to those of either the Musophagidae or of the Galliformes.

Hopkins (1949) suggested that the similarities between the Mallophaga of turacos and galliforms might be due to accidental transfer rather than common ancestry.

Mayr and Amadon (1951: 8) epitomized the uncertainty concerning the relationships of the turacos and cuckoos by noting the "difference of opinion, first as to whether or not the turacos (Musophagidae) should be associated with the Galli, and second whether or not the cuckoos (Cuculidae) are related to the turacos." They thought "it best to place the turacos tentatively near the Galli" but also that "it is entirely possible that the Musophagidae are somewhat primitive relatives of the Cuculidae, so we tentatively follow convention in associating the two families in the same order."

The morphology of the pelvic appendage in *Coccyzus*, *Crotophaga* and *Geococcyx* was described by Berger (1952). He did not speculate on relationships at the level of orders or families but did recommend the placement of *Coccyzus* in a separate subfamily because of its pelvic muscle formula (AXYAm), which differs from the other genera in the Phaenicophaeinae (ABXYAm).

Berger (1953a) found the pterylosis of *Coua caerulea* of Madagascar to be most similar to that of *Geococcyx*, *Crotophaga*, and *Guira*. He (1953b) also studied the appendicular anatomy of *Coua* and found it similar to that of *Geococcyx*.

The muscles of the wing in the American cuckoo genera *Coccyzus*, *Crotophaga* and *Geococcyx* were examined by Berger (1954), who concluded that the differences among them could be explained as adaptations related to their different flight patterns. He suggested that the "differences in flight pattern . . . may best be explained in terms of a progressive reduction in relative wing area and a progressive increase in body size from *Coccyzus* to *Geococcyx*."

Berger (1955) examined the anatomy of the glossy cuckoos and recommended that *Lampromorpha* and *Chalcites* be combined with *Chrysococcyx*. In 1960 Berger compared the myology, pterylosis and syringeal anatomy of the Cuculidae and the Musophagidae and concluded that the turacos should be separated as an order, Musophagiformes. He also reviewed previous classifications of the Cuculidae, pointed out that there is great anatomical diversity among the genera, and decided that Peters' (1940) classification of the cuckoos is unsatisfactory.

Verheyen (1956b,c) reviewed previous anatomical evidence, added data from a primarily osteological study and concluded that the resemblances between the cuckoos and turacos are due to convergence. He believed that the Musophagidae are related to the Galliformes and that the Cuculidae are closest to the Picidae and Coliidae. He divided the Cuculiformes into two suborders, the Centropodes (Centropidae, Phaenicophaeidae, Crotophagidae, Neomorphidae) and the Cuculi (Coccyzidae, Cuculidae). Verheyen proposed that the order Musophagiformes, with its suborders Musophagi and Opisthocomi, be placed next to the Galliformes.

Moreau (1958) reviewed the genera, species, and subspecies of the Musophagidae and recognized 18 species in 5 genera. He discussed some of the opinions concerning the relationships of the turacos to other groups but maintained a neutral position on the question. He suggested, however, that comparisons between the turacos and *Centropus* might be "particularly relevant" in determining the affinities of the Musophagi. Moreau (1964) also presented a synoptic review of the turacos and noted (p. 842) that they "have been associated . . . with either the Galliformes or the Cuculiformes, and have also been exalted to a distinct order, the Musophagiformes (Musophagae of Stresemann)."

Sibley (1960) found the electrophoretic profiles of the egg white proteins of the turacos to be unlike those of the gallinaceous birds. The pattern of *Tauraco corythaix* was similar to that of *Cacomantis merulinus* and that of *Grinifer concolor* resembled that of *Centropus benghalensis*. Sibley stated (p. 243) that "it seems apparent that the coucals . . . are indeed the link between typical cuckoos and turacos." The egg white patterns of the cuckoos were heterogeneous. Those of *Cacomantis* and *Chrysococcyx* were similar. *Clamator*, *Crotophaga*, and *Geococcyx* shared similar patterns and resembled *Centropus*. The pattern of *Coccyzus* differed from those of all these genera.

V. and E. Stresemann (1961a) ascertained the sequence in which the primaries are molted in nearly every genus of the Cuculidae. In the cuckoos the primaries do not molt in the more usual "descending" mode but in the "transilient" mode in which the molt "proceeds by forward or backward leaps across one or more adjoining quills" (p. 330). The variations in molt pattern were considered to be "an important criterion of affinity" within the family and groupings of genera within the Cuculinae were proposed.

The Stresemanns (1966) again reviewed the "transilient" molt patterns in the cuckoos. In the primary molt patterns of the turacos and of the kingfisher *Chloroceryle* they found that the molt occurs in two "action groups"—an outer and an

inner. The sequence is descendent but is usually disturbed by "transilience" as in the cuckoos. In 1969 the Stresemanns described the molts of the genus *Clamator* and found that the primary molt differs from that of *Cuculus*. They concluded that "this confirms the isolated position of *Clamator*" (p. 203.)

SUMMARY. Most authors have thought that the Cuculi and Musophagi are closely related, but their decisions have often been based on tradition rather than on new evidence. A link between the cuckoos and the gallinaceous birds through the Musophagi has frequently been proposed, usually because *Opisthocomus* was considered to be a link. The Cuculi seem to be a rather isolated group and their nearest allies, other than the Musophagi, have been thought to be the Psittaciformes, some Pici-formes, or some Coraciiformes, but there seems to be little solid evidence in favor of any of these proposals.

THE EGG WHITE PROTEIN EVIDENCE

ORDER CUCULIFORMES

FAMILY MUSOPHAGIDAE, Turacos. 3/19, fig. 31.

Species examined: *Tauraco leucotis*, *livingstonii*; *Crinifer concolor*.

FAMILY CUCULIDAE

Subfamily Cuculinae, Cuckoos, Roadrunners. 24/123, figs. 31, 32.

Species examined: *Clamator glandarius*, *levaillantii*, *jacobinus*; *Cuculus canorus*, *solitarius*, *pallidus*; *Cacomantis merulinus*, *pyrrophanus*; *Chrysococcyx cupreus*, *klaas*, *caprius*; *Chalcites basalis*, *lucidus*; *Scythrops novaehollandiae*; *Coccyzus erythrophthalmus*, *americanus*, *melacoryphus*; *Taccocua leschenaulti*; *Tapera naevia*; *Morococcyx erythropygus*, *Geococcyx californianus*; *Centropus rectunguis*, *sinensis*, *senegalensis*, *superciliosus*.

Subfamily Crotophaginae, Anis, Guira Cuckoos, Hoatzins. 4/5, fig. 32.

Species examined: *Crotophaga ani*, *sulcirostris*; *Guira guira*; *Opisthocomus hoazin* (see below).

The egg white patterns of the Cuculiformes are heterogeneous. The simplest pattern is that of the species of *Centropus* and the turaco *Crinifer concolor*. Component 18 is in the usual place, about 1.0 cm anodally from the origin. The conalbumins are not sharply defined and migrate between the origin and Component 18. (In the pattern of *Centropus senegalensis* one of the conalbumin bands migrates cathodally.) These seems to be no well-defined ovomucoid; perhaps it and the ovalbumin merge to form the large component at about 6.0 cm. A well-defined prealbumin is present.

The pattern of *Tauraco leucotis* differs from that of *Crinifer* and *Centropus* in that its conalbumins all migrate cathodally, Component 18 has a greater anodal mobility, and there are distinct ovomucoid and ovalbumin bands. The significance of these differences is unknown. The pattern of *Tauraco* resembles those of some cuckoos, especially *Chrysococcyx*. In the pattern of *Chrysococcyx* the ovalbumin is double and the prealbumin is dense. Component 18 is faint and moves anodally only slightly. The conalbumins are anodal to Component 18. A cathodally migrating lysozyme is present in the pattern of *Chrysococcyx cupreus*. The patterns of *Cuculus* resemble those of *Chrysococcyx* in most respects.

The pattern of *Clamator* is similar to that of *Chrysococcyx*, but is even more complex, with at least four components in the ovalbumin region, excluding a strong prealbumin and an ovomucoid. The identities and homologies of these multiple bands

are uncertain. The Component 18 of *Clamator* is isoelectric under the conditions of separation. It appears on the anodal side of the origin as a thin, dark line.

The patterns of the New World cuckoos *Guira* and *Crotophaga* are similar to each other. They differ from the pattern of *Clamator* in lacking a well-defined ovomucoid, but the mobilities of the conalbumins and of Component 18 are similar to those of *Chrysococcyx*. As in *Clamator* and *Chrysococcyx* there are multiple bands in the ovalbumin region, but the main bands are not so sharply defined, and, in addition, a number of small, fine components appear. The resemblances among the patterns of *Guira*, *Crotophaga*, and *Opisthocomus* are discussed below.

The patterns of *Coccyzus* differ considerably from those of the other cuckoos. The prealbumin occurs in the same area, but the ovomucoid and ovalbumin move more slowly, the latter appearing at about 5.0 cm from the origin. The conalbumins have about the same mobility as in, for example, *Chrysococcyx*. The Component 18 of *Coccyzus* remains at the origin.

The patterns of the Musophagidae are more similar to those of some cuckoos than they are to the patterns of any other group. There is considerable variation among the patterns of the Cuculidae, but the extremes of pattern are bridged by intermediate types.

The patterns of the cuckoos and musophagids do not resemble those of the Psittaciformes, Coraciiformes, Piciformes, or Columbiformes. In the multiple banding of the ovalbumin they superficially resemble some Galliformes, but they differ from them in all other aspects of the pattern.

CONCLUSIONS

The Cuculi and Musophagi are related and should be placed in the same order. We decline, however, to offer an opinion as to the nearest allies of the Cuculiformes on the basis of either the egg white evidence or the evidence from previous studies. The heterogeneity of the Cuculi as expressed by the anatomical as well as the biochemical evidence seems best understood in the light of their apparently long evolutionary history. The anatomical features of the Cuculi are poorly known and detailed study of the family is badly needed.

B. *OPISTHOCOMUS HOAZIN* (HOATZIN)

INTRODUCTION

Order Cuculiformes

Suborder Cuculi

Family Cuculidae

Subfamily Crotophaginae, Anis, Guira Cuckoos, Hoatzins

The above classification represents our opinion concerning the relationships of the hoatzin. We are presenting the data on this species in this special section because the literature is unusually complex and because our concept of its relationships is a departure from past opinions.

The hoatzin has been a taxonomic puzzle ever since its discovery nearly 200 years ago. In general appearance it is often thought to resemble a chachalaca (*Ortalis: Cracidae*) but actually it is astonishingly like the guira cuckoo (*Guira guira*) in color and pattern although much larger in size. The hoatzin is specialized in several ways and these structural peculiarities have made it difficult to prove an alliance to other avian groups.

The hoatzin inhabits the riparian growth along the rivers and streams of northern South America. It feeds, apparently exclusively (Grimmer, 1962), upon plant material which it first breaks down mechanically in its unusually large, muscular crop. Correlated with the large crop is an excavation of the forepart of the sternum and modifications of other portions of the pectoral girdle. The lining of the crop is horny and the true gizzard is much reduced. On the ventral apterium in the breast region there is a large callosity which is often rested against a branch when the bird is perched. Apparently this is correlated with the need to support the filled crop, which must be quite heavy.

The young have two claws on the digits of the wing with which they grasp branches when climbing around before they can fly. The claws are lost by maturity but the adults use their wings for support when moving through the branches. These birds are rather clumsy in their movements through the vegetation, and they fly poorly, but both young and adults swim well.

The birds form large flocks when not breeding and, with the first rains, break up into smaller nesting groups of two to six individuals. The discovery by Grimmer (1962) that the hoatzin forms a communal nesting association is of particular interest because the anis (*Crotophaga*) and the guira cuckoo also build communal nests (Young, 1929; Skutch, 1935, 1966; Chapman, 1938; Davis, 1940a,b).

In the hoatzin the members of the nesting association build a single, flat nest of loosely entwined dry twigs in branches overhanging the water. Mating seems to be indiscriminate (perhaps polygamous?) and all members of the group participate in incubation and care of the young. The two to five eggs are buff-colored with brown or bluish spots, and incubation requires approximately 28 days. The young have two successive coats of down. They are fed, apparently on plant material, from the crops of the adults (Grimmer, 1962; Sick, 1964). Other accounts of the natural history of the hoatzin have been published by Young (1929), Quelch (1890), Goeldi (1896), and Chubb (1916).

HISTORICAL REVIEW OF THE CLASSIFICATION

The hoatzin was originally described in 1776 by P. Müller, who named it *Phasianus hoazin*. Thus, from the beginning of its taxonomic history, it was associated with the galliform birds and the bias in favor of its allocation to that group was established.

Nitzsch (1840) described the pterylosis of *Opisthocomus* and grouped it with *Colius* and *Musophaga* in the family Amphibolae. G. Gray (1844-1849) included the Opisthocomidae, Coliidae, Musophagidae, and Bucerotidae in the tribe Conirostres of his order Passeres.

Huxley (1867) examined only an incomplete skull and the feet of *Opisthocomus*. He found that the slender vomer bifurcates anteriorly in a way unlike that in other birds. The tarso-metatarsus is like that of gallinaceous birds. Taking other evidence into account he assigned *Opisthocomus* to a "special subdivision" of his Schizognathae. Soon thereafter Huxley (1868b) made a complete study of the osteology of *Opisthocomus* and decided that in the majority of its skeletal characters it most closely resembles the Galliformes and Columbiformes. Those characters that differ from the condition in these two orders are either unique to *Opisthocomus* or similar to those

of the Musophagidae. In Huxley's opinion, *Opisthocomus* is a highly modified form derived from a "Gallo-columbine" stock, and he placed it in a monotypic group, the Heteromorphae.

The pelvic muscle formula in *Opisthocomus*, the crotophagine cuckoos and the galliforms is ABXY Am (Garrod, 1879; Beddard, 1898a: 281). Garrod (1879) also pointed out other anatomical similarities to both galliform and cuculiform birds and concluded that *Opisthocomus* is an intermediate form which helps to ally the Cuculidae and Musophagidae to the Galliformes.

P. Sclater (1880) put *Opisthocomus* in a monotypic order which he thought to be most closely allied to the Cracidae but also distantly allied to the Cuculidae and Musophagidae. Reichenow (1882) recognized the family Opisthocomidae within his order Rasores (= Galliformes). Elliott (1885) was reluctant to specify the nearest allies of the hoatzin, and maintained it in a separate order next to his Gallinae.

An account of the myology of *Opisthocomus* by Perrin (1875) noted its similarities to both *Tyto* and *Columba palumbus*. He did not, however, make comparisons to galliform birds or to cuckoos; so his conclusions are meaningless.

In the arrangement of the secondary wing coverts *Opisthocomus* is most like the Cuculidae (Goodchild, 1886).

Seebohm (1888b) enumerated six osteological characters in which *Opisthocomus* differs from the Galliformes and agrees with the Otididae. This evidence prompted him to place *Opisthocomus* in his suborder Grallae, which contained the gruiform birds. The *Opisthocomus* problem continued to perplex Seebohm; it is "in some respects the most aberrant of birds" (1895: 27). In this classification he united *Opisthocomus*, *Psophia*, and the Heliornithidae in a suborder Psophiae of his Galliformes.

Evidence supporting a close relationship between *Opisthocomus* and the galinaceous birds was presented by Fürbringer (1888). He recognized the families Opisthocomidae and Gallidae within his suborder Galliformes. The next closest allies of *Opisthocomus* he believed to be the Columbiformes. He accepted the possibility of a fairly distant alliance between *Opisthocomus* and the Rallidae and an even more remote one to the Tinamidae.

Gadow (1889, 1892, 1893) found that in the following characters *Opisthocomus* resembles:

GALLIFORMES

Precocial young
Fusion of many thoracic vertebrae
Structure of syrinx, palate and feet
Large crop

CUCULIFORMES

Deep temporal fossae
Short mandibular processes
Absence of basipterygoid processes
Internal spine of sternum
Structure of metasternum
Large coracoid
Spotted eggs
Ten rectrices

In the following characters *Opisthocomus* differs from both the Galliformes and the Cuculiformes:

Lack of apteria on sides of neck
Number of cervical vertebrae
Small thoracic haemapophyses
Shape of liver
Modification of crop as digestive organ
Distribution of down on adult

Gadow (1892: 231) believed that "the Coccoyges and Gallidae are intimately connected with each other through *Opisthocomus*." He thought that the Musophagidae were the cuculiform group most like *Opisthocomus* but he placed the Opisthocomi as a suborder of the Galliformes in his classification (1893: 300). This arrangement was adopted by Stresemann (1927-34) and Wetmore (1930). Gadow considered *Opisthocomus* intermediate between the Galliformes and the Cuculiformes and in the latter found more resemblances to the Musophagidae than to the Cuculidae.

In his linear sequence Sharpe (1891) placed the Opisthocomiformes between his Columbiformes and Ralliformes (= Rallidae, Heliornithidae). In his diagram of relationships, however, the Rallidae and Cracidae are closest to *Opisthocomus*, with the Pteroclididae and Columbidae more distant.

With typical prolixity Parker (1891a) offered an account of the embryology and anatomy of *Opisthocomus*. He emphasized what he considered to be the primitive characters of *Opisthocomus* and apparently thought it was at the base of the "Alectoromorphae," a group consisting of the pheasants, quail, sandgrouse, and pigeons. Yet it is clear that Parker was baffled in interpreting the characters of the hoatzin.

Pycraft (1895) corrected a number of points in papers by several previous authors on the pterylography of *Opisthocomus*. There is a "striking general resemblance" in pterylosis, particularly in the distribution of spinal tract feathers, among *Opisthocomus*, *Tauraco*, and *Centropus*, but "it is not improbable that the life-history of *Opisthocomus* is a survival of what was at one time shared by the Galli, since in nestlings of Cracidae and Gallidae the wing exhibits precisely the same phenomena as . . . noticed in *Opisthocomus* . . ." (p. 362). In the end, however, Pycraft declined to offer an opinion on the relationships of the hoatzin.

Beddard (1889a) described the wing of the embryo of *Opisthocomus* and the syrinx and pterylosis of the young and adult. He did not include comparisons to other species. Beddard (1898a) provided a more complete account of the anatomy of *Opisthocomus* and placed it in a separate order between his Galli and Musophagi. In his opinion (p. 285), "the hoatzin . . . forms a well-marked group of birds."

Some aspects of the anatomy of *Opisthocomus*, especially the intestinal tract, were examined by Mitchell (1896b, 1901a). Like Garrod (1879a), Mitchell observed some similarities in the patterns of intestinal convolutions between *Opisthocomus* and the Cuculiformes but he thought that the similarities among *Opisthocomus*, the Pteroclididae, and Columbidae were most striking. Mitchell was impressed by what he considered important differences between *Opisthocomus* and the Galliformes and (1901a: 221) between *Opisthocomus* and the Cuculidae.

Shufeldt (1904b) erected a suborder for *Opisthocomus* within his Galliformes, which also included suborders for the tinamous and hemipodes. In Shufeldt's list *Opisthocomus* precedes the Pteroclidiformes and Columbiformes. He (1918a) described the osteology and other points in the anatomy of a young *Opisthocomus*, but he did not make comparisons to other groups and did not render an opinion on the affinities of *Opisthocomus*.

In British Guiana and Venezuela Beebe (1909) observed some aspects of the behavior of *Opisthocomus*. He described the use of the wing by adults in climbing, and correlated the weak power of flight with the large crop and corresponding reduction in the size of the sternum. Although Beebe's account is largely anecdotal, he was impressed by the similarities between the behavior of *Opisthocomus* and that of the anis (*Crotophaga*: Cuculidae).

Banzhaf's (1929) detailed study of the fore limb of *Opisthocomus* disclosed that the greatest degree of similarity in the osteology, myology, and neurology of the distal part of the wing was between *Opisthocomus* and the Columbidae. *Opisthocomus*

shows considerable likeness to the Galliformes in the pectoral region and upper arm. Banzhaf did not make a formal taxonomic proposal, but he thought that *Opisthocomus* was less closely related to the Galliformes than had Fürbringer and others. Although Banzhaf mentioned comparisons between *Opisthocomus* and some other non-passerine birds, he apparently did not examine any Cuculiformes.

Böker (1929) entertained the idea that *Opisthocomus* might have evolved its peculiar mode of flight and correspondingly strong wing and tail feathers from a South American cuculiform ancestor with a gliding and fluttering flight. To gain insight into the way this might have occurred, Böker examined the owl parrot (*Strigops habroptilus*), which has a parallel enlargement of the crop and reduction of the sternum and associated pectoral musculature. Although Böker concluded from his study of the crop and adaptations for flight that *Strigops* is a modified parrot (which was not in doubt), he was unable to determine the ancestry of *Opisthocomus*.

E. Stresemann (1927-34) retained ordinal status for *Opisthocomus*, but stated that it is closely related to the Galliformes, and attributed the similarities between *Opisthocomus* and the Musophagidae to convergence. *Opisthocomus* was given subordinal rank within the Galliformes by Wetmore (1930, 1934, 1940, 1951, 1960), Peters (1934), Mayr and Amadon (1951), and Storer (1960a).

Lemmrich (1931) found that all of the 10 species of galliforms he studied had 13 to 15 plates in the sclerotic ring of the eye but that *Opisthocomus* had 12. Lemmrich noted that the difference between the galliforms and *Opisthocomus* is "very remarkable" (p. 534, our translation) because there tends to be little variation within a group. There are few other birds with 12 plates but they include *Cuculus* and the parrots.

Opisthocomus is parasitized by five genera of feather lice, of which four are not found on other birds and the other (*Laemobothrion*) is widespread. Thus, according to Clay (1950), the distribution of Mallophaga suggests an "isolated position" for *Opisthocomus*.

Howard (1950) thought that the fossil genus *Filholornis* from the upper Eocene or lower Oligocene of France was allied to both the cracids and the hoatzin. Brodkorb (1964) proposed a new subfamily for *Filholornis* within the Cracidae. A. Miller (1953) described *Hoazinoides magdalenae* from the late Miocene of Colombia on the basis of the posterior portion of a skull. He regarded this species as a primitive member of the Opisthocomidae and interpreted its characteristics as probably indicating a relationship to the Cracidae. Brodkorb (1964) accepted Miller's conclusions and placed the Opisthocomidae next to the Cracidae.

The skull musculature and its innervations in *Opisthocomus* were compared to representatives of the Galliformes, Musophagidae, and Columbidae by Barnikol (1953). Although he found some similarities between *Opisthocomus* and the Musophagidae, he concluded that the hoatzin is an isolated species with no close ties to any of these groups. He presented a table (p. 520) of 40 anatomical characters of *Opisthocomus*. Of these 8 were shared with the Galliformes, 9 with the Columbidae, and 13 with the Musophagidae.

The early stages in the embryonic development of *Opisthocomus* agree with comparable stages of *Gallus gallus* (Parsons, 1954), but other comparisons were not made.

Of 66 osteological characters of the hoatzin that Verheyen (1956c) examined, 50 were shared with the Musophagidae. This evidence led Verheyen to combine the two groups within the order Musophagiformes, which he believed to be allied to the Anhimiformes and Galliformes. Later (1961), "owing to new information," he placed *Opisthocomus* in a suborder of his Galliformes next to the Cracidae.

Hudson, Lanzillotti, and Edwards (1959: Table III) listed 13 aspects of the

pelvic limb musculature in which *Opisthocomus* differs from all Galliformes. Hudson and Lanzillotti (1964: 110) enumerated 21 "important ways" in which the pectoral musculature of *Opisthocomus* is unlike that of galliform birds. They concluded that "*Opisthocomus* has either been erroneously associated with the Galliformes, or has diverged so far from the original ancestral condition, that there is little or no justification for retaining it in the order" (p. 111).

E. Stresemann (1965) and E. and V. Stresemann (1966) discovered that the feathers and molting patterns of *Opisthocomus* differ from all Galliformes in four important aspects:

- 1) flight feathers in the nestling plumage are lacking
- 2) the first flight feathers grow to nearly the size of those of the adults and are not molted before the bird reaches maturity
- 3) both outer secondaries are not shorter than the neighboring ones, and all develop at the same time
- 4) the primaries are not replaced in the sequence characteristic of the Galliformes, but in a continuous stepwise process.

These differences plus those from anatomy prompted E. Stresemann (1965: 64) to conclude: "Wenn *Opisthocomus* mit den Hühnervögeln verwandt ist, dann nur durch Adam und Eva."

SUMMARY. *Opisthocomus* has most frequently been regarded as an ally of the Galliformes, but an examination of the evidence reveals more important differences than similarities. On the other hand, a number of workers have found many resemblances to the Cuculiformes. The Columbidae, Pteroclididae, Rallidae, Otididae, Tinamidae, and Coliidae, among other groups, have been proposed as more distant relatives of the hoatzin.

THE EGG WHITE PROTEIN EVIDENCE

Opisthocomus hoazin, fig. 32.

The egg white pattern of *Opisthocomus* in starch gel differs from those of gallinaceous birds in most respects. It lacks the cathodal lysozyme component that is prominent in most galliform patterns. The Component 18 of *Opisthocomus* has a mobility similar to that of some Galliformes, but it is more concentrated. *Opisthocomus* lacks the distinctive dense cluster of conalbumins characterizing the galliform pattern; instead, the conalbumins appear as indistinct bands on either side of Component 18. The main anodal portion of the pattern of *Opisthocomus* consists of at least three broad merging bands. These proteins migrate faster anodally than, for example, the ovalbumins of megapodes and cracids but slower than those of most phasianids (e.g., *Gallus*, *Phasianus*, *Lophortyx*). A distinct ovomucoid region is not present in the pattern of *Opisthocomus*, thus one of these three broad bands may be an ovomucoid and the others may be ovalbumins. The homologies of the bands are uncertain, but the pattern is unlike those of the Galliformes, in which ovalbumins appear as sharply defined elliptical bands. Anodal to this main region of the pattern of *Opisthocomus* are two prealbumins, the slower one being the more concentrated.

The distinctive egg white pattern of *Opisthocomus* is not identical to that of any non-passerine bird that we have examined, but it does show a number of resemblances to the patterns of some Cuculiformes. The double prealbumins of *Tauraco leucotis*, for example, are identical in their mobilities and concentrations to those of *Opisthocomus*. But the pattern of *Tauraco* differs in having distinct ovalbumin and

ovomucoid regions and cathodally migrating conalbumins. The main anodal staining region in the pattern of *Opisthocomus* is similar to that of the South American cuculids *Guira* and *Crotophaga*. In the patterns of these cuckoos a distinct ovomucoid is not visible; instead there are three, broad, poorly defined bands that have the shapes and mobilities of the corresponding bands in *Opisthocomus*. The mobility of the conalbumins of *Opisthocomus* is like that of *Guira* and *Crotophaga*, but Component 18 of these cuckoos is different, migrating just anodal to the origin. Some other cuckoos (e.g., *Chrysococcyx*, *Clamator*) show multiple bands in the ovalbumin region, but their patterns differ in a number of details from that of *Opisthocomus*. The patterns of other non-passerine groups show little resemblance to that of the hoatzin. We conclude that the pattern of *Opisthocomus* resembles those of the Cuculiformes (especially the South American crotophagine cuckoos) more than it does any member of the Galliformes.

CONCLUSIONS

Opisthocomus is not closely related to the gallinaceous birds and neither is it close to the turacos (Musophagidae). We suggest instead that it is most closely allied to the neotropical Crotophaginae.

ORDER STRIGIFORMES

Family Tytonidae, Barn Owls
Family Strigidae, Typical Owls

Wetmore, 1960

INTRODUCTION

From the earliest times the owls have been recognized as a relatively homogeneous, well-delineated group. Their raptorial adaptations, soft plumage and nocturnal habits were enough to set them apart from other birds but their nearest relatives have been difficult to identify with confidence.

The palate of owls is "schizognathous, with desmognathous tendency" (Gadow, 1892: 249) or "desmognathous" (Beddard, 1898a: 244), and the pelvic muscle formula is A (Garrod, 1874a) or AD (Hudson, 1937), the ambiens being absent. There are two carotids; the basipterygoid processes are functional; flexor tendons Type 1 (Gadow); hypotarsus simple; syrinx bronchial; nares holorhinal, impervious; aftershaft absent or vestigial; primaries 11, secondaries 12-18, rectrices usually 12 (11-13); caeca large; oil gland usually nude; no biceps slip or expansor secundarium; 14 cervical vertebrae.

This incomplete list of characters contains some that agree with those of the Falconiformes and Caprimulgiformes and some that do not. These two groups have been suggested most often as relatives of the owls. However, there is always the possibility that similarities may be due to convergence because of raptorial adaptations in owls and hawks and of nocturnal habits in owls and goatsuckers.

The owls are frequently divided into two groups, one containing the barn owls and grass owls (*Tyto*) and the other the remaining species or "typical" owls. The two groups differ by a large array of characters, some of which are summarized in Table 4.

The principal questions concerning the classification and relationships of the owls are:

- 1) What is the degree of relationship between the Falconiformes and the Strigiformes?
- 2) What is the degree of relationship between the Strigiformes and the Caprimulgiformes, the Psittaciformes, the Cuculiformes and such other groups as have been proposed as possible relatives.

3) Should the barn owls (*Tyto*) be separated as a family or subfamily from the typical owls?

TABLE 4. Characters of Tytonidae and Strigidae

Tytonidae	Strigidae
Palatines straight, nearly parallel, about same length throughout, almost concealing maxillo-palatines	Palatines curved, much expanded posteriorly; maxillo-palatines largely exposed
Prefrontal process of ethmoid thick and rounded	Prefrontal process of ethmoid a thin plate
Interorbital region thick, without fenestra	Interorbital region thin, often fenestrated
Metasternum shallowly two-notched or entire	Metasternum deeply four-notched
Manubrial process absent	Manubrial process present
Sternal crest dilated	Sternal crest narrow
Furcula coalesced with keel of sternum	Furcula incomplete, free from keel of sternum
Third toe as long as second	Third toe much longer than second
Claw of middle toe pectinate	Claw of middle toe not pectinate
No primaries emarginate on inner web	One to six primaries with inner web emarginate
Tenth primary longer than eighth	Tenth primary shorter than eighth
Tarso-metatarsus without bony ring or loop	Tarso-metatarsus with bony ring or loop on under surface of upper end
Feathers of planta-tarsi reversed (pointing upward)	Feathers of planta-tarsi not reversed (pointing downward)
Ventral pteryla with outer branch united to main stem posteriorly	Ventral pteryla with outer branch free from main stem posteriorly
Tail emarginate	Tail rounded
Facial disc heart-shaped	Facial disc more or less circular
Oil gland with two or three filoplumes	Oil gland without filoplumes

SOURCE: modified from Ridgway, 1914: 598.

One of the most confusing nomenclatural problems within the Aves concerns the application of the Linnaean generic name *Strix*. The details are not important for our present purposes but it should be noted that prior to 1910 the barn owls (*Tyto*) were placed in *Strix* or in *Aluco* (see Allen, 1908). Newton (1876) and Coues (1900) also discussed the problem. Mathews (1910: 500) resolved the controversy by calling attention to the availability of *Tyto* Billberg (1828) for the barn owls.

As noted by Coues (1900) the problem involves not only two generic names but also two family names. Before 1910 the barn owl (*Tyto alba*) was usually called *Strix flammea*. Thus the barn owls were the Strigidae and the typical owls were usually designated the Bubonidae or Asionidae. The generic names *Hybris* and *Aluco* were also applied to the barn owls and the family Aluconidae was often employed.

To avoid confusion in the following reviews of the literature we have indicated the currently used synonyms in all quotations.

HISTORICAL REVIEW OF THE CLASSIFICATION

Most of the early writers included the owls in the same group as the hawks and falcons and placed the raptorial birds at the beginning of their sequence of higher taxa. L'Herminier (1827), however, who based his system upon the structure of the sternum

and shoulder girdle, was the first to place the owls in a separate group from the diurnal birds of prey.

Nitzsch (1840) described the pterylography of several species of owls and divided them into two groups, one containing the genera *Hybris* (= *Tyto*) and *Phodilus* (= *Phodilus*) and the other including all other owls. Thus the separation of the barn owls from the typical owls was proposed at an early date. Nitzsch regarded the owls as close allies of the Falconiformes although he noted several differences in pterylosis. He found that the ventral tract in the barn owl is like that of *Cathartes* except that the contour feathers are more numerous and closer together.

Kaup published a series of papers on owls, culminating in his monograph (1859) in which he "reduced the three subfamilies of Bonaparte, the four of G. R. Gray, and the five of J. Cassin into two natural subfamilies of Day and Night Owls, and . . . degraded to the rank of subgenera eleven genera . . ." (p. 258). Kaup relied mainly upon external characters but he examined the skulls of all available genera. He made no statements concerning the relationships of the owls to other groups. His two "natural subfamilies" did not agree with those of most other authors, for in one (Striginae) he placed *Scops*, *Otus*, *Bubo* and *Strix* (= *Tyto*) and in the other (Syrniinae) the remaining genera.

A critical evaluation of Kaup's work was provided by Coues (1879: 746), who noted that Kaup "coined many new generic names . . . several of which have proven available; but his work cannot be considered of great merit or utility, and would be scarcely remembered were it not for the new genera proposed. His classification is hopelessly vitiated by his 'quinarian' freaks, and his way of working out species has the reverse of felicitous result. I should not be disposed to take issue with any one who might go so far as to consider the author in mention a magnificent failure."

Schlegel (1862) proposed a classification dividing the owls into those with ear-tufts—the Oti—and those without ear-tufts—the Striges. This character was used in many other classifications proposed before 1900.

Lilljeborg (1866) placed the Strigidae in his order Accipitres and, using the shape of the facial disc, recognized the subfamilies Surnini, Strigini, and Hybridinae (*Tyto*).

Milne-Edwards (1867-71) supported Nitzsch's separation of the barn owls from the typical owls and later (1878c) considered *Phodilus* intermediate between the two groups.

The owls differ from the other birds of prey "in most important particulars" (Huxley, 1867), yet he designated them all as members of his Aetomorphae (owls, vultures, hawks, falcons), which he called "an eminently natural assemblage" (p. 462).

Garrod (1873d, 1874a) found that the diurnal birds of prey possess an ambiens muscle but that the owls lack it. Although the presence or absence of the ambiens was the basis for Garrod's division of the class Aves into two subclasses he nevertheless placed the Cohort Accipitres, containing the families Falconidae and Strigidae, in the order Ciconiiformes under the subclass Homalagonatae. He indicated the Strigidae as one of "those homalagonatous divisions" that "do not possess the ambiens muscle in any of their genera" (1874a: 116). This may be taken as evidence that Garrod did not place absolute faith in the significance of the ambiens as an indicator of relationships.

Sharpe (1875) regarded the Striges as an order containing two families, the Bubonidae (= Strigidae of Wetmore, 1960) and the Tytonidae (= Tytonidae of Wetmore, 1960) based upon the structure of the feet and the sternum. The Bubonidae were divided into the subfamilies Buboninae and Syrniinae according to the structure of the facial disc and external ear.

The barn owl (*Strix flammea* = *Tyto alba*) should be the type of the Linnaean genus *Strix*, according to P. Sclater (1879), and thus its family, which he separated from the other owls on the basis of characters of the furculum and sternum, should be known as the Strigidae. The family name for the typical owls should be, in Sclater's opinion, the Asionidae, with the long-eared owl (*Asio otus*) being the type. Using characters of the ear opening, feathering on the digits, and the presence or absence of "horns" he divided the Asionidae into the subfamilies Asioninae, Syrniinae, Buboninae, Atheninae, and Nycteiniae. In 1880 Sclater gave ordinal rank to the owls but placed them next to the Accipitres. He suggested that *Pandion* might be intermediate between the groups because it lacks an aftershaft as do the owls.

Reichenow (1882) remained convinced of a relationship between hawks and owls and included the latter in a single family within his order Raptatores.

Shufeldt reported upon the osteology (1881a) and the soft-part anatomy (1889d) of the burrowing owl (*Speotyto*) but provided no conclusions bearing upon the relationships between owls and other groups of birds.

Barrows (1885) recognized two families of owls and placed them in his order Accipitres. He enumerated many characters in which the owls differ from the diurnal raptors, and although he found some aspects in which the owls agree with *Pandion*, he attributed these to coincidence.

Goodchild (1886, 1891) defined an "accipitrine style" of secondary covert arrangement that was shared by the owls, parrots, most Falconiformes, herons, and cormorants.

The similarities between owls and hawks do not constitute proof of close relationship, according to Fürbringer (1888). He found more significant resemblances between the owls, the Caprimulgi, the Coraciidae, and *Leptosomus*, and included these groups in his suborder Coraciiformes. In his opinion, the Coraciiformes occupy a rather isolated position within his order Coracornithes, which includes all groups above the Psittaciformes of Wetmore's (1960) sequence.

The anatomical characters separating the barn owls and the typical owls were reviewed by Beddard (1888b). He listed seven "osteological characters of the genus *Strix* [= *Tyto*] . . . which apparently distinguish it from all others . . ." (p. 340). He also found support for the "division of the Striges into two families" (p. 341) in the structure of the tensor patagial muscles and, to some extent, in the syrinx. However, he admitted that the syringeal differences alone would not be sufficient to justify the division into two families (p. 344) and that there is "a gradual series . . . leading from *Strix* to *Scops*."

Beddard (1890c) also weighed the evidence on the position of the bay owl (*Phodilus badius*) and added new information from osteology and soft-part anatomy. The anatomical data indicated to him that *Phodilus* is related more closely to the typical owls than to the barn owls. He noted that *Phodilus* "does present certain points of resemblance to *Strix* [= *Tyto*]" but that "the structure of *Phodilus* [= *Phodilus*] does not necessitate . . . a separate family . . . or the amalgamation of two generally recognized families into one" (p. 304).

Seebohm (1890a, 1895) placed the owls in the Falconiformes, but expressed doubt on their allocation (1895: 14-15):

It is very curious how many characters the Striges have in common with the Caprimulgi. In both these suborders the oil-gland is nude, and the down in adult birds is restricted to the feather-tracts, and in neither of them is the ambiens muscle present. None of these characters can be regarded as of much taxonomic

value; in many other groups instances are to be found of the independent acquirement or loss of all of them. The similarity of the syrinx in the Striges and Caprimulgi is more important, but appears to me to be far outweighed by the presence of the cere in the Psittaci, Striges, and Accipitres, and the abnormal plantar tendons of the Caprimulgi.

Sharpe (1891) included the owls in his order Accipitriformes. He considered *Pandion* to be the link between the owls and the hawks. He also thought that the owls are allied to the Caprimulgiformes, particularly *Steatornis*.

Gadow (1892) placed the Striges in his order Coraciiformes next to the Macrochires, which included the goatsuckers, swifts and hummingbirds. He found that the owls agreed with the parrots in 22 of his 40 characters and with the cuckoos in 28 (p. 235). He did not give the score for the owl-goatsucker comparisons. In 1893 he made further critical comparisons between the owls and other groups. Like Fürbringer he could not support a close relationship of the owls to the other birds of prey and he concluded (p. 240): "The nearest relatives of the owls are the Caprimulgi, especially *Podargus* and also *Steatornis*, in spite of its frugivorous habits; then follow the Coraciae, and finally the Cuculi" (transl.).

Until the classifications of Fürbringer (1888) and Gadow (1892) the owls had usually been placed with or near the falconiforms. According to Beddard (1898a: 252), the alliance of the owls "to the picarian birds (in a wide sense)" had been "hinted at by Garrod and Newton" and "given a practical shape in the classifications of Fürbringer and Gadow." Beddard (p. 253) agreed with the separation of the owls from the diurnal birds of prey and concluded that the differences between them "are as great as those which separate any two groups of carinate birds." He noted (p. 243) that the goatsuckers "seem to be most nearly allied" to the owls.

The great influence of Fürbringer and Gadow upon their successors is again indicated by the virtually universal acceptance of an alliance between owls and goatsuckers that is found in most of the present classifications (e.g., Wetmore, 1960; Mayr and Amadon, 1951).

The pterylography of certain owls and goatsuckers was studied by H. Clark (1894). He remarked upon the presence of 11 primaries in owls in contrast to 10 in the goatsuckers and presented drawings and descriptions of the pterylosis of several American genera. He concluded "that the Caprimulgi are related to the Striges, and not very distantly either—probably a branch from the early part of the Strigine stem" (p. 572). He reviewed the opinions of Sharpe (1891), Garrod (1873d) and Parker (1889b), which were opposed to his conclusions, and, while stating that his study revealed "some surprising similarities" between the two groups, cautiously decided that "perhaps, however, it is only an extraordinary case of what may be called 'analogous variation'" (p. 572).

Pycraft wrote two extensive papers on owls, the first (1898a) on their pterylography and the second (1903b) on osteology. His pterylographic investigations confirmed the main conclusions of Nitzsch (1840) except that he found "numerous small but very real differences by which not only genera but even species may be distinguished." He was critical of Kaup's (1862) work but reviewed more favorably the proposals of Nitzsch, Newton (1871-74), Sharpe (1875), and Gadow (1893). Pycraft's study of owl pterylography did not lead him "to any very startling results" (p. 263) but he proposed a classification with two families, the Asionidae [= Strigidae] containing all except the barn owls, which were placed in the Strigidae [= Tytonidae]. He (p. 268) evaluated the pterylographic evidence for the relationships between owls and other orders and found points favoring alliances to both the falconiforms and

caprimulgiforms. Although Gadow (1893) concluded that the owls are most closely related to the caprimulgiforms, Pycraft avoided taking a firm position.

The pattern of intestinal coiling in the owls is little modified from that of a "coraciform-cuculiform metacentre" (Mitchell, 1901a). Beddard (1910), however, disagreed with Mitchell's conclusions and with those of Gadow (1889). Beddard stated (p. 90): "The older opinion as to the Owls, that which placed them close to the Accipitres and not in the neighborhood of various Picarian genera, is most certainly justified by the close similarities in the mode of arrangement of the intestinal loops. At the same time, it is also easy to distinguish these two groups by the small but constant characters afforded by the ileo-duodenal ligament."

Pycraft (1903a) studied the pterylography of *Phodilus badius*, concluding that the species is a member of "the subfamily Asioninae, among which it stands as a somewhat aberrant genus with leanings towards *Asio*" (p. 46). He also found that the form of the external ear in *Phodilus* is unlike that of any other owl but "more nearly like that of *Asio* than . . . of any other genus." In a footnote (p. 46) Pycraft wrote that "there is nothing . . . in the pterylosis of this bird [*Phodilus badius*] which . . . resembles that of *Strix* [= *Tyto*]. Nitzsch, as Beddard has pointed out, seems to have imagined that a resemblance of the kind existed." And, finally, Pycraft stated that *Phodilus* "is not a near ally of *Strix* [= *Tyto*], as has been contended on more than one occasion" (p. 47). The "remarkable character" of the external ear of *Phodilus* caused Pycraft (1903a: 47-48) to revise his 1898 classification of the Asionidae. The new version placed *Asio*, *Syrnium*, *Photodilus*, *Bubo*, *Scops*, *Ninox* and *Sceloglaux* in the subfamily Asioninae.

Shufeldt's (1904b) "supersuborder" Strigiformes contained the families Bubonidae and Strigidae (= *Tyto*). The Strigiformes are preceded by the Psittaciformes and followed by the Caprimulgiformes.

From his studies of feather structure Chandler (1916: 372) concluded:

Although in the great length of the pennula and resulting softness of the plumage the Caprimulgi resemble the Striges, the details of structure, in so far as they differ in these suborders from that of typical Coraciiformes, are not the same, and it is only reasonable to suppose that the similarities are due to parallel evolution and that there is no closer relationship shown between these two groups than between either of them and other coraciiform groups.

E. Stresemann (1927-34) gave *Tyto* only subfamily status in the Strigidae. He did not believe in any close relationship between the owls and the Falconiformes and thought that the nearest allies of the owls are probably the Caprimulgiformes.

Hudson (1937) discovered large differences between the pelvic muscles of owls (*Bubo*, *Otus*) and those of the Caprimulgidae (*Chordeiles*) but he did not examine the myology of other caprimulgiforms (Aegothelidae, Podargidae), which may be closer to the owls.

Glenny (1943b) dissected the carotid arteries in the barn owl (*Tyto*) and seven species of North American Strigidae; all have two carotids as do the Falconiformes. This condition was earlier noted by Garrod (1873d) and is also found in the Caprimulgidae and Steatornithidae.

The evidence from the Mallophaga was presented by Clay (1950: 44): "The owls are parasitized by two genera; the affinities of one (*Strigiphilus*) are unknown, the other (*Kurodia*) is found elsewhere only on the Falconiformes."

Verheyen (1956a, 1961) divided the Strigiformes into the usual two families, Tytonidae and Strigidae, with the latter composed of the Asioninae, Phodilinae and Striginae. He noted that *Tyto* has been separated from the other owls on the basis of many characters, to which he added the weakly developed hyoid, the long, thin

mandibular rami, and the very short internal process of the mandibular articulation. Verheyen placed *Steatornis* in his Caprimulgiformes but considered it intermediate between them and the owls.

Sibley (1960) found that the paper electrophoretic patterns of the egg white proteins support a relationship between the Strigiformes and Caprimulgiformes. He also noted, "The egg-white profile of *Tyto* . . . is distinctive but clearly similar to the other genera and neither supports nor refutes the separation of the two families" (p. 242).

Mees (1964) revised the taxonomy of the owls of Australia and kept the Tytonidae and Strigidae as separate families because there "does not seem to be any advantage in grading down the two families" to subfamilies.

In a comparison of the structure of the syrinx in *Tyto*, *Phodilus* and several genera of strigids, A. Miller (1965) concluded "that *Phodilus* has more points of resemblance to the Strigidae than to *Tyto* although there are some departures from the Strigidae which are suggestive of *Tyto*. *Phodilus* is not, however, clearly intermediate between them" (p. 538).

Marshall (1966) assembled data on the skeleton, syrinx, voice, facial disc, ectoparasites, and behavior of *Phodilus*. He stated that the bay owl shows "departures from Strigidae, even greater removal from Tytonidae, and nothing clearly intermediate" and recommended "placing *Phodilus* in its own family, the Phodilidae" (p. 238). He also concluded that *Otus scops* and *O. flammeolus* are separate species because the voices are so different that "they cannot be in the same species" (p. 240). Marshall (1967) relied primarily upon personal field observations and upon vocalizations by the screech owls (*Otus*) in a study of their species limits in North and Middle America. This paper did not consider higher category problems.

W. Bock and McEvey (1969b) reported on the os prominens (a large, hook-shaped, sesamoid bone in the tendon of the M. tensor patagii longus of the Strigidae). The os prominens is absent in *Tyto* but present in many hawks. The shape of the os prominens and the relationships of the tendons and ligaments to this bone differ in owls and hawks, so Bock and McEvey claimed that this structure does not indicate affinity between the two groups. They also discussed the osseous arch on the radius that serves as the attachment for Mm. pronator profundus and extensor indicus. They found the osseous arch in the strigid owls as well as in *Tyto*. Because it is apparently a unique structure to strigiform birds, Bock and McEvey felt that it indicates that *Tyto* is closely related to the other owls.

An important piece of evidence concerning the relationships of *Tyto* has been provided by Flieg (1971), who reported a cross in captivity between a male barn owl (*Tyto alba*) and a female striped owl (*Rhinoptynx clamator*). The female laid four eggs, two of which were fertile, developing to about the fifteenth day. Flieg observed, "Since the two families of Strigiformes are thought to be taxonomically distinct, this record of hybridization may be of some value" (p. 178).

SUMMARY

The owls have most often been thought to be allied to the Falconiformes or the Caprimulgiformes, and it has been implied that they may be related to both. The Cuculiformes, Psittaciformes, and some Coraciiformes (Coraciidae, Leptosomatidae) have also been proposed as relatives of the owls.

A relationship to the diurnal birds of prey was espoused by the early workers, who were clearly influenced by the similar raptorial adaptations of both groups. Following the work of Fürbringer and Gadow the hawk-owl similarities were at-

tributed entirely to convergence and the owls were thought to be most closely allied to the Caprimulgiformes.

As noted in the section on Falconiformes, evidence from the trigeminal musculature has reopened the possibility that the owls may be related to the falcons.

The evidence from hybridization indicates that *Tyto* is closely related to the other owls, but various opinions have been expressed as to the nearest relatives of *Phodilus*, the only other problem genus of the Strigiformes. However, since it is now clear that *Tyto* and the strigids are closely related there is little reason to assume that *Phodilus* is actually very distant from the other owls. Its differences from them are clearly due to special adaptations but do not necessarily indicate a large genetic gap.

THE EGG WHITE PROTEIN EVIDENCE

ORDER STRIGIFORMES

FAMILY TYTONIDAE, Barn Owls. 1/11, fig. 32.

Species examined: *Tyto alba*.

FAMILY STRIGIDAE, Typical Owls. 16/123, figs. 32, 33.

Species examined: *Otus scops*, *asio*, *leucotis*; *Bubo virginianus*, *lacteus*, *sumatranus*; *Ketupa ketupu*; *Ninox strenua*, *novaezeelandiae*; *Athene noctua*, *brama*; *Speotyto cunicularia*; *Ciccaba woodfordii*; *Strix seloputo*, *aluco*; *Asio otus*.

The similarities between the egg white pattern of the Strigiformes and those of the Falconidae have been discussed under the latter. Patterns typical of the Strigidae are those of *Asio otus* and *Speotyto cunicularia*. In these patterns Component 18, about 1 cm from the origin, is rather diffuse. The conalbumins are also indistinct and migrate on both sides of Component 18. The ovomucoid is a single but not sharply defined band at about 5 cm from the origin. Between the conalbumins and the ovomucoid is an area that stains lightly. The ovalbumin is distinctly double, the slower component being more concentrated. All strigid owls that we have examined fit this pattern, with only slight mobility differences in the conalbumins and ovomucoids among species.

The pattern of *Tyto* differs from those of the Strigidae in having a third component in the ovalbumin region. The mobility of these three bands is slightly less than in the patterns of the strigid owls. The pattern of *Tyto* thus bears a strong resemblance to those of the Strigidae and also, as noted earlier, to those of *Falco*.

Apart from the falcons the only group to which the egg white patterns of the owls show a resemblance is the Caprimulgidae.

CONCLUSIONS

The barn owls (*Tyto*) are closely related to the other owls and do not deserve familial or subfamilial distinction from them. Tribal separation may be justified.

The closest relatives of the owls, judging from all the evidence, seem to be the Caprimulgiformes. We decline, however, to make a firm proposal in this regard, since the old question of an owl-falcon relationship has been reopened by anatomical as well as biochemical evidence. The exact degrees of relationship of the owls to the falcons and to the caprimulgiforms are yet to be determined.

ORDER CAPRIMULGIFORMES

Suborder Steatornithes

Family Steatornithidae, Oilbirds

Suborder Caprimulgi

Family Podargidae, Frogmouths

Family Nyctibiidae, Potoos

Family Aegothelidae, Owlet-frogmouths

Family Caprimulgidae, Goatsuckers

Wetmore, 1960

INTRODUCTION

All of the caprimulgiforms are specialized for crepuscular or nocturnal activity and many of them feed by capturing insects on the wing. They therefore combine, whether by convergence or common ancestry, the morphological characters of the owls and the swifts. Similarities to the trogons and to other groups have also been suggested.

The question of degrees of relationship among the caprimulgiform groups has also stimulated many studies. The oilbird, *Steatornis*, which feeds upon the fruits of a variety of palms, Lauraceae, Burseraceae and Araliaceae, and which nests in caves, has become highly specialized. Nevertheless, there seems to be no doubt of its caprimulgiform affinities. Similarly, the frogmouths (*Podargus*) seem, at least superficially, to be owl-like and may possibly be the link between the two groups. However, *Podargus* feeds upon non-flying animal prey and its heavy bill is adapted to this mode of life. The potoos (*Nyctibius*) and owlet-frogmouths (*Aegotheles*) are also specialized and each resembles the owls in certain adaptations. The goatsuckers, Caprimulgidae, are looked upon as the core of the order because they were the first group to be taxonomically defined (being the only one to occur in Europe) and because they are the largest and most widely distributed group.

The questions to be answered concerning the Caprimulgiformes are the following:

1) Are the caprimulgiforms most closely related to the owls, the swifts, the trogons or to some other group?

2) Are the groups currently included within the order more closely related to one another than to the members of some other order?

HISTORICAL REVIEW OF THE CLASSIFICATION

Possibly the first to place the goatsuckers and the owls together was Moehring (1752). His Accipitres included *Strix*, *Caprimulgus*, *Psittacus*, *Falco*, *Aquila* and *Vultur*. However, in most of the earlier classifications the goatsuckers were associated with the swifts, which were, in turn, considered to be allied to the swallows. Such an arrangement was followed by Linnaeus (1758), Brisson (1760), Illiger (1811), Merrem (1813), Temminck (1820), L'Herminier (1827), Wagler (1827), G. Gray (1840), Cabanis (1847), Fitzinger (1856-65), Carus (1868-75), and Sundevall (1872).

Nitzsch (1840) recognized that the owls and the goatsuckers may be related but in his classification they were placed in separate groups, with the Caprimulgidae associated more closely with the swifts, rollers, cuckoos, etc. Lilljeborg (1866) placed the Caprimulgidae between the owls and the swifts. In Huxley's (1867) classification the Caprimulgidae, Cypselidae (swifts) and Trochilidae comprised his "Group Cypselomorphae." He thought that *Aegotheles* is most like the swifts, that *Caprimulgus* resembles the trogons, and that *Podargus* is distantly related to the owls. He considered the Cypselomorphae to be close to the passerines and included both groups in his suborder Aegithognathae.

P. Sclater (1866a,b) based a subdivision of the goatsuckers upon characters of the sternum, the digits and the bill. He divided the Caprimulgidae into the Steatornithinae (*Steatornis*), Podarginae (*Podargus*, *Batrachostomus*, *Nyctibius*, *Aegotheles*) and Caprimulginae (typical goatsuckers).

Steatornis closely resembles the Strigidae in its pterylosis (Garrod, 1873c). *Steatornis* agrees with the Strigidae, Caprimulgidae, Coraciidae, Momotidae, and Galbulidae in having two carotid arteries, well-developed caeca, a nude oil gland and in lacking the ambiens muscle. Garrod thought that *Steatornis* was best retained in a monotypic family but declined to offer an opinion as to its nearest relatives.

In Garrod's system (1874a: 117-18) the goatsuckers and oilbirds are associated with the passerines, trogons, puffbirds, bee-eaters, jacamars, rollers, motmots and todies in the order Passeriformes, subclass Anomalogonatae. The swifts and hummingbirds are in the adjacent order Cypseliformes and the owls are next to the Falconidae in the "Cohort Accipitres" of the order Ciconiiformes, subclass Homalagonatae. Garrod placed the owls among the "homalagonatous" birds although, like the goatsuckers, they lack the ambiens.

P. Sclater (1880) followed Huxley (1867) and associated the goatsuckers with the swifts and hummingbirds, and the owls with the diurnal birds of prey. Reichenow (1882) did much the same.

Newton (1884) separated the owls from the falconiforms and placed them near *Steatornis* "which, long confounded with the Caprimulgidae . . . has at last been recognized as an independent form, and one cannot but think that it has branched off from a common ancestor with the owls. The Goatsuckers may have done the like, for there is really not much to ally them to the Swifts and Humming-birds . . . as has often been recommended" (p. 47). In a footnote (p. 47) Newton remarked upon the "resemblance in coloration between Goatsuckers and Owls" and recommended that it "be wholly disregarded."

Although he underscored the differences in palatal structure among *Steatornis*, *Podargus*, and *Caprimulgus*, Stejneger (1885) nevertheless believed them to be closely related. He erected the superfamily Coracioideae within his large order Picariae to contain the Steatornithidae, Podargidae, Caprimulgidae (including *Nyctibius*), Leptosomatidae, and Coraciidae. To him the palate of *Caprimulgus* was similar to that of passerines, and several structural aspects of *Steatornis* seemed to suggest an alliance to the owls.

Shufeldt (1885b) compared the skeletons of hummingbirds, goatsuckers and swifts and concluded that the caprimulgids *Nyctibius* and *Steatornis* are closely related to the owls but that the swifts are closer to the swallows and unrelated to the goatsuckers.

The syrinx, visceral anatomy and appendicular myology of some caprimulgiforms were examined by Beddard (1886a). He concluded "that *Steatornis* is a peculiar type of Goatsucker and needs a special subfamily to itself. . . . A second subfamily will include *Podargus* and *Batrachostomus*, while *Aegotheles* ought perhaps to be" in a third subfamily. A fourth subfamily was proposed for *Caprimulgus*, *Chordeiles* and *Nyctidromus*. Beddard noted that his study supported the classification proposed by P. Sclater (1866a).

Goodchild had difficulty in proposing the nearest relatives of the caprimulgiform birds on the basis of his studies on the arrangement of the secondary coverts. In his 1886 paper he stated that the Caprimulgi do not resemble the swifts and hummingbirds but are more like woodpeckers. On the other hand, *Steatornis* appears most like the cuckoos. In 1891 he defined a "cuculine style" which he believed to be a modification of the covert arrangement of the passerines. This style was shared by the Cuculidae, Caprimulgidae, Steatornithidae, and Podargidae.

In 1888 the basis for the present association (e.g., Wetmore, 1960) of the owls and goatsuckers was established by Fürbringer when he placed the Caprimulgi (Caprimulgidae, Steatornithidae, Podargidae) next to the Striges (Strigidae) in his suborder Coraciiformes of the order Coracornithes. He attributed the resemblances between the Caprimulgi and the swifts to convergence.

Gadow's (1889) study of the intestinal convolutions led him to state that the affinities of the owls "rest with the Coraciidae and Caprimulgidae combined" and that "the Caprimulgidae, Cypselidae [= Apodidae], and Trochilidae agree very much with each other. . . . The Cypselidae and Caprimulgidae are somewhat more closely related to each other, and the latter (including *Podargus*) turn towards the Owls." He thought that the trogons were also part of this assemblage and especially close to the goatsuckers and rollers because they too are "isocoelous" and have large caeca "like the Coraciidae, Caprimulgidae and Striges . . ." (p. 315).

Within his subclass Coraciiformes Seebohm (1890c) diagnosed an order Picariae as follows: "Hallux always present, and connected with the *flexor perforans digitorum*, and not with the *flexor longus hallucis*: no ambiens muscle" (p. 203). Within this group he recognized a suborder Coraciae, which contained the Cypselidae (= Apodidae), Caprimulgidae, Steatornithidae, Podargidae, Leptosomatidae, Coraciidae, and Meropidae. In 1895 Seebohm gave the Caprimulgi subordinal rank in his order Coraciiformes next to the suborder Picariae, which included the Coraciiformes of Wetmore (1960), the Coliidae, and Apodidae.

Sharpe (1891) included the caprimulgiform birds in his large order Coraciiformes and recognized as suborders the Steatornithes, Podargi, and Caprimulgi. He separated the Caprimulgi from the others, however, by several suborders representing the Coraciiformes of Wetmore (1960) and placed them next to the swifts and hummingbirds. Sharpe further noted: "It was an old fancy that, because of a certain similarity in the style of plumage and because also of their crepuscular habits, the *Caprimulgi* and the *Striges* were nearly allied; and though this idea is now scouted, it would seem that the nearest approach to the *Striges* . . . will be found in the *Steatornithes* . . ." (p. 65).

Gadow (1892) set up an order Coraciiformes with suborders Striges (Strigidae), Macrochires (Caprimulgidae, Cypselidae, Trochilidae), Colii (Coliidae), Trogones (Trogonidae), Coraciae (five families). In 1893 Gadow gave the Caprimulgi subordinal rank in his Coraciiformes and expressed the opinion that, other than the owls,

their nearest allies were first the Coraciidae, then the Cypseli. Essentially the same arrangement was adopted by Wetmore (1930) and is widely used at the present time.

Pycraft (1898a: 268) considered Garrod's (1873c) conclusion that "in its pterylosis . . . *Steatornis* resembles the Strigidae much more than any of the allied families" to be an overstatement of the available facts.

The syrinx of the caprimulgiforms is "highly characteristic" (Beddard, 1898a: 235) and he further stated:

Like the nearly related (?) cuckoos, we have both the tracheo-bronchial and the purely bronchial syrinx. Indeed, the stages are almost identical in the two groups. *Cuculus* and *Caprimulgus* correspond with a tracheo-bronchial syrinx; then we have *Centropus* and *Podargus*, and finally the culmination in *Crotophaga* and *Steatornis* of a syrinx furnished with a membrana tympaniformis, which does not commence until many rings below the bifurcation of the tube, the intrinsic muscles being attached to the first ring which borders upon it.

Beddard realized that the syringeal structure of the caprimulgiforms also resembles that of the owls, and he believed the owl-nightjar alliance to be closest. He seemed to be most impressed by the similarities in the intestinal tracts of the two groups. Mitchell (1901a) concluded that the intestinal tract of the Caprimulgiformes is "archecentric" (generalized) and that the alimentary canals of the Coraciidae, Coliidae, Apodiiformes, and Passeriformes could be derived from it. In a later paper Beddard (1910) no longer seemed to regard the similarities in the intestinal tracts of owls and caprimulgiforms as significant. He found more resemblances between the owls and the hawks.

H. Clark (1901a) reported on the pterylosis of *Podargus* and reviewed the pterylography of other caprimulgiforms. He disagreed with Nitzsch (1840) who said that the pterylosis of *Podargus* is like that of *Caprimulgus*. According to Clark, "the pterylosis of *Podargus* is very distinctive" (p. 167) and intermediate between that of the caprimulgids and the owls. He concluded that "the accumulated evidence thus confirms the view that Goatsuckers and Owls are near relatives" (p. 170). Clark also disputed Nitzsch's view on the pterylosis of the swifts and concluded that the swifts and goatsuckers are "strikingly different" in their pterylosis and that there seem "to be no connecting links" between them.

Chandler (1916) mentioned several points of similarity in the feather structure between caprimulgids and owls, but he believed that the softness of the contour feathers in the two groups is due to convergence. Although he regarded both groups as members of the Coraciiformes (*sensu lato*), he did not think that they are each other's closest allies.

A specimen of *Nyctibius griseus* was dissected by Wetmore (1918), who also reviewed the characters of other caprimulgiforms. He agreed with Gadow (1893) that "the Nyctibiidae seem to form an intermediate group" between the Podargidae and the Caprimulgidae and that the Aegothelidae "serves to narrow the gap still more." Wetmore proposed (p. 586) "that the suborder Nycticoraciae of the Order Coraciiformes may be divided into two superfamilies, the Steatornithoidae with the single genus *Steatornis* and the Caprimulgoidae with the families Podargidae, Nyctibiidae, Aegothelidae, and Caprimulgidae."

W. D. Miller (1924a) determined the condition of the vestigial eleventh primary or "remicle" in various groups of birds. In owls and *Podargus* the remicle is normally present. In the swifts, and ordinarily in the caprimulgids, there is only a single small feather, presumably the eleventh lower covert, on the outer side of the tenth primary. Miller (p. 315) noted: "However, in the Australian nightjar, *Eurostopodus mystacalis*

. . . both the covert and remicle are present. . . . Thus the nightjars are moved a trifle nearer the owls and farther from the swifts."

In E. Stresemann's (1927-34) opinion, the nearest relatives of the Caprimulgiformes are the owls.

Hudson (1937: 77) concluded that a "study of the musculature of the pelvic limb in a goat-sucker (*Chordeiles*) and in certain owls (*Bubo* and *Otus*), fails to disclose any unusual similarity. The formulae are very different (AXY for *Chordeiles* and AD for the owls) and there are numerous other striking differences in the pelvic musculature." The myological formula of the Caprimulgidae also differs from that of the swifts (A) and from that of the cuckoos (AXYAm).

In an examination of the arterial arrangements in the heart region in 12 species of Caprimulgiformes, Glenny (1953b) observed that the Steatornithidae and Caprimulgidae have two carotids, the Podargidae and Nyctibiidae only one, the left. These findings confirmed those of Garrod (1873c) and Wetmore (1918).

Verheyen (1956a) analyzed a long list of anatomical characters in a study of the owls, trogons and goatsuckers. He concluded that these three groups are related to one another and he proposed a classification in which the order Caprimulgiformes contains the suborders Podargi, Caprimulgi, Trogones and Steatornithes. The Strigiformes are the adjacent order. In 1961 Verheyen removed the trogons from the Caprimulgiformes and placed them in the preceding order, the Coraciiformes. Otherwise he did not change the sequence.

Sibley (1960) found that the electrophoretic patterns of the egg white proteins of caprimulgids and owls are similar and that "*Steatornis* is clearly caprimulgiform" (p. 242). There was "nothing in the egg-white protein patterns to support the suggestion that goatsuckers are related to the swifts," to the trogons or to the Coraciiformes.

An extensive study of *Steatornis* in Trinidad was carried out by Snow (1961, 1962) over a period of three and one-half years. Although his own research was concerned with ecology and behavior he reviewed the entire literature on the oilbird and noted (1961: 27-28) "that *Steatornis* is almost certainly closer to the caprimulgiform birds than to any other group, but even to them the relationship is very distant, while in certain characters they resemble the owls, perhaps due to convergence."

SUMMARY

A relationship between caprimulgiforms and owls has been proposed repeatedly but the possibility of convergence has haunted its post-Darwinian advocates. The swifts, which, like the goatsuckers, have the large mouths and long rictal bristles of aerial insectivores, have also been proposed as allies by many authors. Many other groups, including the trogons, rollers, cuckoos, piciforms and even the passerines, have been suggested as caprimulgiform relatives.

A consensus has been difficult to achieve although an owl-caprimulgiform alliance has clearly been the most frequent assumption in avian classifications. That the oilbirds, potoos, frogmouths, owlet-frogmouths and goatsuckers are allied most closely to one another has not been seriously challenged.

THE EGG WHITE PROTEIN EVIDENCE

ORDER CAPRIMULGIFORMES

FAMILY STEATORNITHIDAE, Oilbird. 1/1, fig. 33.

Species examined: *Steatornis caripensis*.

FAMILY PODARGIDAE, Frogmouths. 1/12, fig. 33.

Species examined: *Podargus strigoides*.

FAMILY NYCTIBIDAE, Potoos. 1/5, fig. 33.

Species examined: *Nyctibius griseus*.

FAMILY AEGOTHELIDAE, Owlet-frogmouths. 1/8, fig. 33.

Species examined: *Aegotheles cristatus*.

FAMILY CAPRIMULGIDAE, Nightjars or Goatsuckers. 13/67, fig. 33.

Species examined: *Chordeiles minor*; *Podager nacunda*; *Nyctidromus albicollis*; *Nyctiphrynus ocellatus*; *Caprimulgus vociferus*, *longirostris*, *parvulus*, *macrurus*, *tristigma*, *europaeus*, *rufigena*; *Scotornis fossii*; *Semeiophorus vexillarius*.

In the egg white pattern of the Caprimulgidae the conalbumins migrate between the origin and Component 18. Component 18 stains much less intensely than in many groups. The ovomucoid is not well defined; it migrates 5.5–6.0 cm from the origin, being somewhat variable in its position. The ovalbumin is distinctly double in the pattern of *Caprimulgus longirostris*. The pattern of *Semeiophorus vexillarius* probably has three bands in the ovalbumin, but they do not resolve well under the conditions of separation.

The pattern of *Nyctibius griseus* agrees with those of the Caprimulgidae in the number and mobility of all components. The pattern of *Steatornis* is also like that of the Caprimulgidae, the only difference being a less concentrated ovomucoid.

The pattern of *Podargus strigoides* differs from that of the Caprimulgidae. The conalbumins migrate anodal to Component 18, but such shifts in the relative positions of these fractions are not uncommon in other groups of birds. The ovomucoid has a mobility like that of, for example, *Chordeiles minor*, but the mobility of the ovalbumin is shifted cathodally so that it is close to the ovomucoid. The ovalbumin contains two bands. At the position of the most anodal ovalbumin band in the caprimulgid pattern *Podargus* has a less intense component which is either a third ovalbumin or a prealbumin. In all aspects the pattern of *Aegotheles* agrees with that of *Podargus*. The pattern of *Podargus* and *Aegotheles* seems thus to be a modification of that of the caprimulgids, but the significance of the differences is not known.

As mentioned previously, the patterns of the Caprimulgidae, *Steatornis*, and *Nyctibius* are most like those of the owls. They have less concentrated ovomucoids, and the ovalbumins move slightly less anodally than the respective components in the strigid pattern. In the arrangement of components and in the poorly defined bands, even in fresh material, the patterns of the Caprimulgiformes are like those of the Picidae. This resemblance is not so strong as to the owl pattern. The patterns of the caprimulgiforms are unlike those of the Cuculidae, Apodidae, and Trogonidae.

CONCLUSIONS

The Caprimulgidae, Nyctibiidae, and Steatornithidae are closely allied. The Podargidae and Aegothelidae seem closely related and, although caprimulgiform, comprise an outlying group.

The nearest allies of the Caprimulgiformes are the Strigiformes. Perhaps both groups are best included in a superorder, but we decline to make a proposal in this matter, pending further investigation of possible owl-falcon relationships.

ORDER APODIFORMES

Suborder Apodi

Family Apodidae, Swifts

Family Hemiprocnidae, Crested-Swifts

Suborder Trochili

Family Trochilidae, Hummingbirds

Wetmore, 1960

INTRODUCTION

The controversy concerning the relationships of the swifts and hummingbirds began at least 150 years ago and continues to the present day. Some characters seem to indicate that the two groups are related, but in many other characters they differ from one another. The swifts also show a number of superficial similarities to the swallows (*Hirundinidae*), *Caprimulgiformes*, and even to the trogons.

The principal questions concerning the higher category relationships of these groups are the following:

- 1) Are the swifts and hummingbirds related more closely to one another than either is to any other group?
- 2) Are the swifts related to the passerines, the goatsuckers, the colies or the trogons?
- 3) If the hummingbirds are not related to the swifts then which are their closest living relatives?

HISTORICAL REVIEW OF THE CLASSIFICATION

In many of the earlier classifications the swifts and swallows were placed together, usually well separated from the hummingbirds, which were commonly associated with *Certhia*, *Upupa*, *Nectarinia*, etc. This situation is found in the arrangements proposed by, for example, Linnaeus (1758), Brisson (1760), Illiger (1811), Merrem (1813) and Temminck (1820). However, L'Herminier (1827) examined the structure of the

sternum and shoulder girdle and was apparently the first to detect a possible alliance between swifts and hummingbirds. Berthold (1831) also studied the sternum and compared some 130 species. He saw the similarities noted by L'Herminier but concluded that the sternum is unreliable as a source of data for classification rather than that swallows are passerine and that swifts are related to hummingbirds.

Nitzsch (1840) placed the swifts and hummingbirds together in the Macrochires with the goatsuckers nearby. In G. Gray's (1844-49; 1869-71) classifications the swifts were placed near the swallows and goatsuckers, and the hummingbirds with the honeycreepers (*Coereba*) and honeyeaters (*Meliphagidae*).

It was J. Müller's (1847) study of the syrinx that provided the basis for the separation of the swifts from the swallows and allied them with the goatsuckers.

Cabanis (1847), who based his classification primarily on the number of flight feathers and the tarsal envelope (podotheca), recognized the swallows as oscines (after J. Müller, 1846) and placed the swifts and hummingbirds together with the goatsuckers in his Macrochires.

Wallace (1863) also believed that the hummingbirds are related to the swifts and not to the passerine sunbirds, which they resemble superficially.

P. Sclater (1865a) studied the sternum and foot structure in the swifts and proposed their division into two subfamilies, Cypselinae and Chaeturinae. He was confident that "the Swifts have no relationship whatever with the Swallows" (p. 593).

The Cypselomorphae of Huxley (1867) contained three families, the Trochilidae, Cypselidae, and Caprimulgidae, and Huxley believed that the swifts are "very closely related" to the swallows among the passerine birds. Although Huxley considered the palate of these groups to be aegithognathous, Parker (1875a) found that the palate of the nightjars and hummingbirds is schizognathous. It was Parker's opinion that the swifts and hummingbirds are not closely allied and that the swifts have indirect ties to the passerines, particularly to the swallows.

In Garrod's (1874a) classification, based upon the pelvic musculature, the swifts (*Cypselinae*) and hummingbirds (*Trochilinae*) are the only subfamilies in his family Macrochires, order Cypseliformes. Garrod thought that the differences between swifts and hummingbirds "are only of subfamily importance. The formula is A; the tensor patagii brevis and the pterylosis are characteristic, as is the sternum; and there is only a left carotid (except in *Cypseloides*)" (p. 123). Garrod (1877c) marshaled evidence from pterylography, the structure of the sternum, syringeal morphology, intestinal coiling, deep plantar tendons, number of rectrices, and the insertion of the patagial muscles to support his contention that swifts are not closely allied to swallows. In all these characters the swifts resemble the hummingbirds.

P. Sclater (1880) associated the Trochilidae, Cypselidae (= Apodidae) and Caprimulgidae in the suborder Cypseli, and Reichenow (1882) followed the same basic arrangement but designated the group as the order Strisores.

Stejneger (1885: 437) reviewed the differences between swifts and swallows, as follows:

Externally they may be easily distinguished; the swifts by having ten primaries, not more than seven secondaries, and only ten tail-feathers, while the swallows have but nine primaries, at least nine secondaries, and twelve tail-feathers. The swifts have also the dorsal tract bifurcate between the shoulders, while in the swallows it is simple. Internally they differ in a great number of points, but we shall only mention that the swifts have a pointed manubrial process and no posterior notches to the sternum, while the swallows have the manubrium bifurcate, and the posterior border deeply two-notched; the former have a myological formula $A\div$, the latter $AXY\div$; the former are synpelmous, the latter are

schizopelmous; the former have a peculiar arrangement of the tensor patagii brevis, the latter have the general arrangement of the Passeres . . . ; the former have a simple syrinx without intrinsic muscles, the latter have a very specialized syrinx; the former are without caeca, the swallows possess them, etc., the total effect being that the swifts are Picarians, and the swallows are Passeres.

Stejneger also enumerated the characters in which swifts and hummingbirds agree, and he placed both groups in the superfamily Micropodoideae in the order Picariae, after the trogons and at the end of his sequence of non-passerines.

Shufeldt (1885b) examined the osteology of the hummingbirds, goatsuckers and swifts. “. . . The Swifts are essentially modified Swallows, and, as the family Cypselidae, they belong, in the order Passeres, next to that group” (p. 914). He repeated this position the following year (1886d: 503), noting that “the humerus is highly pneumatic in *Trochilus*, which . . . is not the case among the Cypselidae, these latter agreeing with the Swallows . . . in having non-pneumatic humeri.”

Lucas (1886) disagreed with those advocating the association of the swifts with the swallows (namely, Sharpe, Parker, and Shufeldt) and supported “Huxley’s union of Hummingbirds and Swifts” (p. 444). Lucas compared the skulls and other skeletal elements of a hummingbird, a swift and a swallow and concluded that the skull of the swifts indicates “affinities not only with the Passeres but with the Hummingbirds and Goatsuckers . . .” and that “the remaining portions of the skeleton . . . point to the relationship of *Chaetura* with *Trochilus*, while between these birds and the Passeres stand the Goatsuckers” (p. 451).

In his usual turgid prose Parker (1889c:2) disagreed with P. Sclater (1865) and Garrod (1877c) and agreed with Shufeldt (1885b) that the “Swallow and the Swift are near akin,” basing his opinion upon palatal similarities, proportions of the wing bones, and other skeletal characters.

Goodchild’s studies on the arrangement of wing coverts (1886, 1891) convinced him that the swifts and hummingbirds are closely allied. He demonstrated that they were unlike the passerines in this respect but was unable to suggest their nearest allies.

Fürbringer (1888) found no reason to dispute a close relationship between the swifts and hummingbirds and set up a separate gens—the Macrochires—for them. He believed that they and the colies are closely related to a pico-passerine assemblage.

In a lengthy paper on the “Macrochires” Shufeldt (1889e) reviewed available evidence and added the results of his own study of the anatomy of the cedar waxwing (*Bombycilla cedrorum*), *Trogon mexicanus* and *puella*, four species of caprimulgids, two of swifts, seven of hummingbirds and six of swallows. The anatomy of the cedar waxwing was studied as the basis for comparisons with the “structure of a suitable and average Oscinine bird” (p. 387). Shufeldt’s conclusions were:

1) *Trogon* shows no evidence of close relationship to the Trochili or to the Caprimulgi.

2) The Caprimulgi are most closely related to the owls and “have no special affinity with the Cypseli, much less with the Trochili” (p. 388).

3) The swallows “possess . . . the . . . characters of the . . . Passerine stock. . . . They are true Passeres considerably modified . . . [by] the adoption of new habits . . .” (p. 388–89).

4) “Our modern Swifts were differentiated from the early Hirundine stock” (p. 390).

5) Swifts differ from hummingbirds in their habits, nidification, feeding behavior, external characters and body form, pterylosis, skull and body skeleton, wing structure, pelvic structure, respiratory system, visceral anatomy and digestive system.

6) Swifts and hummingbirds are unrelated to one another and the two groups

should be placed in separate orders. The Cypseli "would be found just outside the enormous Passerine circle, but tangent to a point in its periphery opposite the Swallows. . . ." The Trochili belong in a separate order (p. 391).

Shufeldt believed that the similarities between swifts and hummingbirds were superficial because "truly related organizations *never* exhibit such an array of inharmoniously associated sets of morphological characters" (p. 391).

Lucas (1889) reviewed certain skeletal elements of the swifts, including "*Dendrochelidon*" (= *Hemiprocne*), and proposed a division of the superfamily Micropodoidea into two families: Micropodidae for the typical swifts and Dendrochelidonidae (= Hemiprocniidae) for the crested swifts. "In some points" the crested-swifts "incline towards the Goatsuckers" (p. 12).

Seebohm (1890a,c) agreed with Shufeldt (1885b, 1889e) that the swifts and hummingbirds are not closely allied. He cited the structure of the deep plantar tendons as evidence for making the Trochili a suborder of the Pico-Passeres, next to the Eurylaemi. In his system the swifts are placed next to the caprimulgiform birds in the suborder Coraciae of his subclass Coraciiformes. In 1895 Seebohm maintained the Trochili as a suborder of the Passeriformes but arranged the swifts, colies, and coraciiform birds in the suborder Picariae of the Coraciiformes.

The suborders Caprimulgi, Cypseli, Trochili and Colii were arranged by Sharpe (1891) in a linear series in his order Coraciiformes, with the Trogones the next order after the Colii.

In a monograph of the hummingbirds, especially the North American forms, Ridgway (1892: 290) wrote: "The Humming Birds and Swifts . . . agree in numerous anatomical characters, and there can be no doubt that they are more closely related to each other than are either to any other group of birds. In fact, except in the shape of the bill and the structure of the bones of the face, the Humming Birds and Swifts present no definite differences of osteological structure."

Gadow's (1892) classification was much like that of Sharpe. It included an order Coraciiformes with suborder Striges (Strigidae), Macrochires (Caprimulgidae, Cypselidae, Trochilidae), Colii (Coliidae), Trogones (Trogonidae) and Coraciae (five families). This sequence of groups was followed by Wetmore (1930, 1960). Gadow (1893) gave the Caprimulgi separate subordinal rank, yet he believed them to be closely related to the Cypseli (swifts and hummingbirds). He also thought that the colies are somewhat more distant allies of the Cypseli.

Lucas (1895b) corrected Gadow's (1894: 617) diagram of the deep plantar tendons of hummingbirds. Gadow (1895) agreed, added further corrections and noted that the actual arrangement in the hummingbirds indicates the "last remnants of a regular four-split condition of the tendon" of the flexor longus hallucis and that this shows that the hummingbirds are "still nearer related to the Cypseli" than previously demonstrated.

Lucas (1895c) also examined the deep flexor tendons of the crested-swift *Hemiprocne* ("*Macropteryx*") and found them to differ from those of the typical swifts. In the crested-swift the flexor hallucis gives off a branch to the hallux and then continues "to blend, not with the undivided tendon of the flexor communis, but with that branch of it which goes to supply the fourth digit." This arrangement "does not agree with any of the seven modifications of . . . these tendons . . . figured by Garrod. But it is . . . like . . . *Scopus umbretta* figured by Beddard (P.Z.S. 1891, p. 18, fig. 46)" (p. 300).

"There are still to be found among living systematic ornithologists some who contend that the Humming-birds (*Trochili*) are more or less nearly related to the Swifts (*Cypseli*) . . ." wrote Shufeldt (1893b). He then proceeded to belabor Coues and Ridgway for "keeping alive the false idea that Swifts and Humming-birds" are related

to one another. On Shufeldt's side of the argument were W. K. Parker and T. H. Huxley. These three believed that the swifts are related to the swallows and that the affinities of the hummingbirds were simply not known. Shufeldt listed 61 differences between the swifts and hummingbirds, accompanied by a running fire of scathing comments directed at his opponents. He summarized (p. 100) his polemic by submitting the "61 important structural differences . . . to the thoughtful systematist . . . confident . . . that after their weight has been duly appreciated there will no longer be any doubt . . . that not only is a typical Swift a widely different kind of bird from a Humming-bird, but that . . . the Swifts are but greatly modified Swallows. . . ."

But Shufeldt's crusade against the infidels was not yet over, for H. Clark (1902a) reopened the question of hummingbird-swift relationships. Clark's discussion was based only upon pterylosis and he concluded that the two groups were so similar that they are probably related. Shufeldt's scathing reply (1902c), published only two months later, quickly dismissed Clark's question, data, and arguments as incompetent or irrelevant. In his final sentence (p. 48) Shufeldt agreed with Clark's (1901a) view concerning the relationship between owls and goatsuckers "but one must get the ancient picarian bee completely out of one's anatomical thinking-cap before cypseline-trochiline comparisons can be made without bias and without prejudice."

Clark (1902b) published a brief reply to Shufeldt's attack but waited four more years until he had assembled a much larger array of pterylographic evidence before returning to the battle. Clark's (1906) paper on the feather tracts of swifts and hummingbirds reviewed the history of the debate with Shufeldt and called attention to errors in Nitzsch's figures that Shufeldt had used to bolster his own arguments. Clark presented data on the pterylosis of 10 species of swifts and 21 species of hummingbirds, 17 of which he studied personally. From comparisons of the two groups Clark concluded that the pterylosis of the swifts and hummingbirds is sufficiently similar "to give support to the view that they have a common ancestry . . ." (p. 89). On the contrary, "the pterylosis of the Caprimulgi" is not "sufficiently similar to that of swifts or hummingbirds" to indicate common ancestry (p. 90). And that, apparently, concluded this particular debate for neither Shufeldt nor Clark seems to have published additional evidence on it.

The alliance of the swifts and hummingbirds in the Macrochires was accepted by Beddard (1898a). He reviewed the arguments on their relationships and noted (p. 229) that although Shufeldt (1885b, 1886d) "is disinclined to allow a very near affinity between the birds, it is undeniable that there are resemblances."

Lucas (1895a) found that the name *Dendrochelidon* was preoccupied by the name *Macropteryx* for the crested- or tree-swifts (= *Hemiprocne*) and, along with a notice of the nomenclatural change, presented some additional data on their anatomy. The deep plantar tendons of *Hemiprocne* were found to have certain resemblances to those of hummingbirds. Lucas concluded that the differences between the crested-swifts and the typical swifts "are greater than those existing between any two families of Passeres" (p. 157).

Lucas (1899), in his report on the myology of a cloud swift ("*Hemiprocne*" = *Streptoprocne zonaris*), pointed out that the peroneus longus, a muscle found in the passerines, is absent in *Streptoprocne*. Furthermore, the deep plantar tendons in the cloud swift differ from those of other swifts in that "while the muscle which ordinarily works the front toes, the flexor perforans, is present it has no separate tendon, but is attached to the muscle of the first digit, *flexor longus hallucis* . . . below this single tendon sends off four slips, one to each digit, thus presenting the simplest condition possible and literally realizing Gadow's statement that the *flexor longus hallucis* is really a common flexor of all digits" (p. 78).

From his investigations on the avian intestinal tract Mitchell (1896a, 1901a)

showed that swifts and hummingbirds have nearly identical conditions. He noted several differences between them and the passerines and concluded (p. 256) that "the conformation of the Cypseli and Colii may also be an apocentric derivative of the Caprimulgid form, the apocentricity in both consisting of an immense reduction in the length of the whole gut, with degeneration of the caeca so that no vestige of them is left, and with obliteration of the loops in Meckel's tract. . . ."

Following a detailed study of wing structure of swifts and hummingbirds, with particular emphasis on the innervation of muscles, Buri (1900) concluded that the two groups are closely allied. In his opinion, the colies are the next closest relatives of swifts, and the Caprimulgi are more distant.

Thompson (1901) described the pterylosis of the giant hummingbird (*Patagona gigas*) and compared it to that of the nightjar *Caprimulgus macrurus* and the swiftlet *Collocalia spodiopygia*. ". . . I am inclined to think that the facts of pterylosis, so far as they go, tend to justify the association of the Humming-birds with the Goatsuckers and Swifts, and, if anything, to bring them somewhat nearer to the former than the latter of the last two. But I am bound to confess that the evidence is confused and the judgment far from clear. There are many resemblances and many differences, and we are not yet in a position to decide what proportion of weight several characters deserve" (p. 324).

A classification primarily based upon pterylosis was proposed by H. Clark (1901b). "If one will compare a plucked Swift and Swallow . . . it will at once appear that . . . the pterylosis is strikingly different . . ." (p. 372-73). He considered the Cuculiformes, Coraciiformes and Passeriformes to have a similar type of pterylosis. He noted (p. 381) that "Nitzsch's . . . figures are often faulty, and . . . the relationship between the Goatsuckers and Swifts . . . are not borne out by examination of better material. . . ."

In 1902 Fürbringer again judged the swifts and hummingbirds to be related and placed them as adjacent families in his "Gens" Macrochires, with the Passeres on one side and the Colii on the other. He (p. 704) observed that Shufeldt's (1893b) list of 61 differences between swifts and hummingbirds could easily be increased but that their quality would not be improved sufficiently to provide a basis for the wide separation of the two groups.

Without comment Shufeldt (1904b) assigned the swifts and hummingbirds to separate orders, placing the Trochiliformes between the Todidae of the Halcyoniformes and the Bucconidae of the Jacamariformes, and including the Cypseliformes between the Piciformes (= Picidae only) and the Eurylaemiformes.

The question of generic limits in the Trochilidae, a problem still very much with us, was brought into focus in 1909 when Taylor called attention to the fact that many hummingbird genera are based upon the same characters used to differentiate species. Taylor advocated the mergence of hybridizing species into the same genus, a viewpoint in accord with that of many modern systematists (Sibley, 1957; Banks and Johnson, 1961; Short and Phillips, 1966; Lynch and Ames, 1970), but Ridgway (1909) disagreed.

Chandler (1916) described the fine structure of the feathers of swifts and hummingbirds. Although he did not directly approach the problem of the relationships of these two groups, he indicated his belief that the Trochilidae are closely allied to the Passeriformes. In his "phylogenetic tree" (p. 391) he placed the swifts with the caprimulgidiformes.

E. Stresemann (1927-34) included the swifts and hummingbirds in the same order but did not suggest ties to any other groups.

Lowe (1939b) took issue with Parker (1875a), Beddard (1898a), and others who claimed that the palate of hummingbirds is schizognathous. Lowe argued that

the hummingbird palate represents a "low" degree of aegithognathism and then re-defined the order Passeriformes to include the swifts, the hummingbirds, and the Pici. Although he ranked the swifts and hummingbirds in separate suborders, he believed them to be closely allied. ". . . It seems to me almost unbelievable that their likeness could be due to convergence in two unrelated groups. The similarities exhibited are altogether too many, too exact, and too universal, affecting as they do a complete system of muscles, nearly all of them highly specialized, and in addition an osteological and intestinal system" (p. 327). Lowe believed that the swifts and hummingbirds had evolved from the "generalized trunk" of the passerine line but was unable to indicate a passerine group to which they are most closely related.

Wetmore (1947) reviewed the nomenclatural history of the generic names *Micropus* and *Apus* and provided a basis for the recognition of *Apus* Scopoli as the type genus of the swifts.

The Mallophaga of swifts are uninformative concerning relationships, but those found on hummingbirds are found also on passerines (Clay, 1950).

Lack (1956a) reviewed the 10 species of the genus *Apus* and (1956b) the genera and nesting habits of swifts. He recognized eight genera in the Apodidae, plus *Hemiprocne* (with three species), in the Hemiprocnidae. He did not comment upon the problem of the relationships between swifts and other groups.

The paper electrophoretic patterns of the egg white proteins of swifts and hummingbirds indicated to Sibley (1960) that the two groups are related. The patterns also suggested passerine affinities.

Wetmore (1960) included the swifts (Apodi) and the hummingbirds (Trochili) as suborders in his Apodiformes and placed the order between the Caprimulgiformes and the Coliiformes. He favored giving family status to the Hemiprocnidae because of the following points (p. 15):

The skull in the Hemiprocnidae is quite distinct in the general form of the cranium and in the development of the nasals, vomer, and palatines. The hypotarsus has a tendinal foramen (like that found in hummingbirds), and the plantar tendons have the flexor longus hallucis connected with the branch of the flexor perforans digitorum, which extends to the fourth digit. Coupled with this there may be noted the curious nest, which, fastened to the side of a branch, is barely large enough to contain one egg, and the further fact that these birds perch regularly on branches and twigs in trees.

The classification of the subfamily Chaeturinae was reviewed by Orr (1963), who questioned Lack's (1956b) classification of the group but did not deal with higher category relationships.

Verheyen (1956h), once again deluded by convergence, assigned the hummingbirds to his order Upupiformes, especially to the vicinity of the wood-hoopoes, *Phoeniculus*. The swifts were placed in an independent order, the Apodiformes, near the Caprimulgiformes. In his later arrangement (1961) Verheyen made adjacent but separate suborders in the Coraciiformes for the swifts and hummingbirds, placing the Trochili next to the Upupae and the Apodi next to the Trogones.

Simonetta (1967) concluded that the swifts are related to the Caprimulgiformes through *Hemiprocne* and *Aegotheles*. The hummingbirds cannot be included in the same order with the swifts, in Simonetta's view, but he declined to suggest their nearest allies, pending study of other groups. His conclusions were derived from studies of the morphology and mechanics of the skull.

Cohn (1968) attributed the skeletal similarities between swifts and hummingbirds to convergence. In her study of the flight mechanism of these birds she found

that to derive hummingbirds from a swift-like ancestor would require at least ten reversals of evolutionary trends. She believed that the hummingbirds may be closest to the stem of a pico-passerine assemblage leading to the New World non-oscines but did not suggest the nearest allies of the swifts.

In his review of the classification of the swifts Brooke (1970) considered all levels of their relationships. Although unsure as to "whether the Apodi are an order or a suborder and, if the latter, of which order" he observed (p. 13) that Lowe's (1939b) "view that they are aberrant passerines has not found favour, and opinion is swinging away from the view that they are related to the Trochili (e.g., Cohn, 1968)." Brooke "noted a resurgence of the view that they are related to the Caprimulgi (Dr. C. T. Collins and Dr. P. Brodkorb, pers. comm.) but . . . we have not yet got the evidence to state this. They can stand as a separate order but this does not answer the question of their affinities . . ." (p. 13). Brooke maintained the families Apodidae and Hemiprocnidae and recognized two subfamilies, Cypseloidinae and Apodinae in the Apodidae. The Apodinae were further divided into three tribes. He recognized 83 species of swifts in 19 genera, including *Hemiprocne*.

Among the differences between the Cypseloidinae and Apodinae given by Brooke (p. 23) were the number of peaks in the paper electrophoretic patterns of the egg white proteins (Sibley, 1960: 282). Brooke is correct in his observation of the apparent differences between the patterns but we cannot be certain that the differences are correlated with the two subfamilies until several species in each group have been examined. The egg white of only one cypseloidine species was available in 1960.

The highly modified condition of the splenius capitis muscle which occurs in swifts and hummingbirds, and in a less developed form in the Aegothelidae, was described by Burton (1971). He suggested that this modification may in some way be useful in aerial feeding by swifts. Its development in both swifts and hummingbirds, which have different feeding habits, seems to indicate a common ancestry. Other aerial feeding groups such as the Glareolidae, Meropidae, Galbulidae, Tyrannidae and Muscicapidae do not have this modification.

SUMMARY

The resemblances between the swifts and swallows have long been attributed to convergence, but investigators have been unable to prove whether the similarities between the swifts and the hummingbirds are due to convergence or to common ancestry. Since the time of Fürbringer and Gadow most authors have accepted the union of the two groups but several studies have reopened the question, which must still be considered unanswered.

Apart from the hummingbirds the nearest relatives of the swifts have been thought to be the Caprimulgiformes, the colies, and the trogons. The evidence for any of these suggestions is not compelling, but neither is the evidence against them. The nearest allies of the hummingbirds have been postulated to be among the Piciformes or Passeriformes, but again the definitive evidence in support of one or another group has not been presented.

THE EGG WHITE PROTEIN EVIDENCE

ORDER APODIFORMES

FAMILY APODIDAE, Swifts. 13/16, fig. 34.

Species examined: *Collocalia fuciphaga*, *esculenta*; *Streptoprocne zonaris*;

Aerornis semicollaris; *Chaetura pelagica*, *brachyura*; *Apus melba*, *apus*, *pallidus*, *caffer*, *horus*, *affinis*; *Cypsiurus parvus*.

FAMILY HEMIPROCNIDAE, Crested Swifts. 1/3, fig. 34.

Species examined: *Hemiprocne longipennis*.

FAMILY TROCHILIDAE, Hummingbirds. 16/319, figs. 34, 35.

Species examined: *Glaucis hirsuta*; *Threnetes ruckeri*; *Phaethornis guy*, *pretrei*; *Colibri coruscans*; *Chrysolampis mosquitus*; *Chlorostilbon aureoventris*; *Thalurania glaucopis*; *Hylocharis cyanus*; *Aphantochroa cirrochloris*; *Topaza pella*; *Sappho sparganura*; *Loddigesia mirabilis*; *Myrtis fanny*; *Calypte costae*; *Selasphorus platycercus*.

The egg white patterns of the swifts are simple. Four or five conalbumins migrate anodally 2–3 cm from the origin and apparently mask Component 18. In many swifts there is but a single band in the "ovalbumin region" about 6 cm from the origin. In some species (e.g., *Apus apus*, *caffer*, *horus*) a second component appears cathodal to the main band, and in the pattern of *Streptoprocne zonaris* there are two well-separated bands.

The pattern of *Hemiprocne longipennis* matches well those of *Chaetura brachyura* and other swifts, except for a slightly faster ovalbumin.

Over a wide range of genera the egg white patterns of the hummingbirds are uniform. They show the same number and mobilities of the conalbumins as the swifts, but, in some, Component 18 can be identified cathodal to the conalbumins. About 4 cm anodally from the origin the hummingbirds have a band which presumably is ovomucoid. At about 7 cm is a double ovalbumin, the more anodal band staining darker, and in most species a prealbumin is also present.

The patterns of the hummingbirds differ considerably from those of the swifts, especially in the ovalbumin region. The pattern of *Streptoprocne zonaris* comes closest to matching those of the hummingbirds. The patterns of the hummingbirds somewhat resemble those of the woodpeckers, but the latter do not show the well-defined subdivision of the ovalbumin. The patterns of the hummingbirds do not closely resemble those of the passerines; those of the swifts do so only in the slow mobility of the ovalbumins. Among the non-passerines the pattern of the swifts resembles those of the colies, but the significance of this similarity is unknown. The pattern of the swifts seems to have little in common with those of the Caprimulgiformes.

CONCLUSIONS

The degree of relationship between the swifts and hummingbirds remains unclear. The egg white evidence does not support a close relationship, yet it is possible to derive the patterns of the swifts and the hummingbirds from a common type. Because it is not possible on the basis of all available evidence to defend a close alliance between either the swifts or the hummingbirds and any other passerine or non-passerine group, we recommend no change in the classification. This problem is one of the most interesting ones in non-passerine systematics and deserves further attention. Any detailed study of this question should take into account the resemblances between the egg white patterns of the swifts and the colies.

ORDER COLIIFORMES

Family Coliidae, Colies or Mousebirds

Wetmore, 1960

INTRODUCTION

The colies or mousebirds of Africa are a strange and interesting group of six species, remarkable for many peculiarities of habit and structure that set them well apart from all other birds. Generally drab in colouring, they are characterized by their long stiff tails and pronounced crests, and all are of a similar shape and size. Together their ranges cover virtually all of un-forested Africa south of the Sahara, and in some habitats the birds are very common. . . .

In behaviour and ecology the colies . . . are gregarious, living in small parties the year round, even while breeding . . . ; and they feed in similar ways. They are . . . frugivorous, but . . . not exclusively so, eating much foliage and . . . nectar of flowers. [Rowan, 1967: 64.]

The palate in the colies is "indirectly desmognathous" and the vomer is "reduced to the merest vestige" (Pycraft, 1907b: 253). The first and fourth toes are reversible, the foot thus being "pamproctactyl"; nares holorrhinal and impervious; pelvic muscles AXY; no basipterygoid processes; 13 cervical vertebrae; metasternum with two deep incisions on each side; furcula with hypocleideum; only left carotid; latissimus dorsi metapatagialis absent; syrinx tracheo-bronchial; no caeca; thick skin; large after-shaft present; no down feathers; plumage soft and hair-like; 10 primaries; 10 secondaries; rectrices variable, 10-12; eutaxic; oil gland feathered; molt of primaries and secondaries usually regular, sometimes irregular, tail molt irregular (mostly after Murie, 1872a; Garrod, 1876e; Beddard, 1898a; Pycraft, 1907b; Rowan, 1967).

According to Gadow (1892) the flexor tendons are Type 5 but Pycraft (1907b: 237-38) disputed this and described a unique arrangement in the colies which he believed was derived from the same type found in swifts and hummingbirds.

The foregoing synopsis of the natural history and anatomy of the colies provides

a basis for comparisons with other groups and indicates their unique combination of characters.

There is only one question concerning the colies: to what other living group are they most closely related? The candidates for this distinction include most of the "higher" non-passerines and the passerines, as will become apparent in the following review of the classifications of the colies.

HISTORICAL REVIEW OF THE CLASSIFICATION

In some of the earlier classifications *Colius* was, not surprisingly, allied with the passerines (Linnaeus, 1758; Brisson, 1760; Illiger, 1811). Nitzsch (1840) placed the colies with the Musophagidae and *Opisthocomus* in his Amphibolae, and Cabanis (1847) followed the same plan. Huxley (1867) saw the desmognathous palate and included the Coliidae in his Coccoyomorphae next to the Musophagidae.

After a study of its osteology, Murie (1872a) advocated separate ordinal rank for *Colius*. He was convinced that *Colius* does not belong in the Passeriformes or Psittaciformes, nor close to the woodpeckers or the hoatzin. He found some characters suggesting an alliance with the rollers and turacos but was not convinced of their value. He summarized his study as follows (p. 277-78):

The facts are these: if we take one set of regional characters—the feet, the head, the breast bones, the pelvis, and so on—we can place it in as many different groups; we can even trace Raptorial kin; so that it is hard to say where *Colius* could not be wedged in, and plausibly too. Not only is it entitled to be considered aberrant, but to afford the strongest proof of the interlinking of type—not in the chain-series so often advocated, but, like the Isle of Man tripod coat-of-arms, kicking its legs about, and whichever alighting upon, there it stands.

But if, in the true spirit of ornithology, we take the bird in its completeness, it will be allowed it does not so closely resemble any acknowledged individual group as to come under its definition.

Without advocating its proper place, I propose equally to exclude it from the old Fissirostral and Scansorial, and the Passerine groups, the recent Coccoyomorphae and Coracomorphae. It, as I conceive, is equally with the Woodpeckers and Goatsuckers, Celeomorphae and Cypselomorphae, annectant betwixt the Coccoyomorphae and Coracomorphae.

Garrod (1876e) examined several aspects of the anatomy of *Colius*. He found that the sternum most closely resembles that of the Capitonidae and that *Colius* is like the swifts in having a "tough skin." Only the left carotid artery is present, and the pelvic muscle formula is *AXY*, the same as that found in most Piciformes and Passeriformes. The arrangement of the plantar tendons, in Garrod's opinion, is exactly like that in the Alcedinidae. (But see Pycraft, 1907b, and plantar tendon section of the Introduction to this volume.) Garrod concluded that the colies are allied on one hand to the Picidae, Capitonidae, and Rhamphastidae and on the other to the Alcedinidae and Bucerotidae. He gave the colies family rank in the order Piciformes, which he defined as birds lacking the ambiens muscle and caeca and possessing a tufted oil gland.

P. Sclater (1880) placed the Coliidae in his suborder Anisodactylae, which in-

cluded the coraciiforms, *Podargus*, and *Steatornis*. Reichenow (1882) included the Coliidae between the Musophagidae and Crotophagidae in his order Scansores.

Several opinions on the relationships of *Colius* were reviewed by Stejneger (1885) but he did not offer any original thoughts. He placed the colies in a superfamily between the superfamilies Coracioideae (rollers and caprimulgiforms) and Alcedinoideae (most coraciiforms) in his order Picariae.

The Macrochires (swifts and hummingbirds) and Pico-Passeres are the nearest relatives of the colies, according to Fürbringer (1888), who found a number of characters indicating a distant, but undeniable, affinity. In his linear sequence he gave the colies a "gens" (Colii) of their own between the Macrochires and the Trogones. With these groups in his order Coracornithes Fürbringer included the passerines, the piciforms and the cuculiforms.

Gadow (1889) found the intestinal convolutions of the colies to be "isocoelous" and he placed them nearest the Musophagidae and Trogonidae.

The suborder Halcyones in the order Picariae of Seebohm (1890c) contained the Todidae, Momotidae, Coliidae, and Alcedinidae. In 1895 Seebohm added to this assemblage (which he renamed the suborder Picariae) the Cypselidae, Todidae, Coraciidae, and Bucerotidae.

Sharpe (1891) put the colies in a suborder in the Coraciiformes and noted that "the Colies must also stand alone, a little group, between the *Cypseli* and the larger group of *Halcyones* etc., but without any very near relatives" (p. 66).

Gadow (1892) compared the colies with other groups, using his 40 or more characters. He noted (p. 235): "Notoriously difficult forms, as, for instance, Trogons and Colies, naturally caused more trouble than others, since the number of comparisons had to be increased." In his classification (1892: 250) the Colii were ranked as a suborder between the Macrochires (goatsuckers, swifts, hummingbirds) and the Trogones in the order Coraciiformes, which, in addition, included the owls and the coraciiforms. In his discussion of the colies Gadow (1893: 252-54) made the following observations (our translation):

1) The colies are typically coraciiform in their intestinal coiling and flexor tendons.

2) The colies are related to the trogons.

3) Even more closely related are the goatsuckers, hummingbirds and swifts, especially the swifts and the African Caprimulgidae.

4) The pterylosis of *Colius* is very similar to that of swifts and hummingbirds.

5) The palate of *Colius* is "directly desmognathous" as in most Coraciae. The palatal differences between the colies and goatsuckers are not important since both schizognathy and desmognathy occur in the Caprimulgi.

6) The condition of the spina externa of the sternum also indicates that *Colius* is related to the Coraciae rather than to the Caprimulgi and the swifts.

7) The smallness of the procoracoid is like that of *Trogon*, but that of the Momotidae, Passeriformes and swifts is also smaller than that of most Coraciiformes.

8) The deep, doubly cleft sternum, is relatively primitive and stands at the same level as that of the trogons. The solidier sternum of goatsuckers and swifts is reflected in their better flying abilities.

Gadow's conclusions (1893: 254) were that *Colius* differs in many ways from the goatsuckers and swifts but is nevertheless related most closely to them, especially to the swifts. He also considered the trogons to be members of this group.

Beddard (1898a) reviewed the characters of the colies and listed his Colii between the Alcedines and Trogones without significant comment concerning their relationships.

Mitchell (1901a: 251) found the intestinal tract of *Colius* to be "relatively

shorter and wider than in any other bird that I have examined, and this modification, no doubt due to small size and frugivorous habit, has obliterated practically the underlying morphological form." He derived the intestinal tract arrangements of the colies, swifts, and hummingbirds from that of the Caprimulgidae.

The colies ranked as a "supersuborder" between the Cocygiformes (Cuculiformes) and Picariformes (Piciformes) in Shufeldt's (1904b) classification.

Pycraft (1907b) was able "to add some new facts, as well as to correct . . . errors of interpretation" made by his predecessors (p. 229). His results may be summarized as follows:

1) The pterylosis of colies and swifts show "a remarkable and significant likeness" (p. 249).

2) Down feathers are lacking and the oil gland is tufted.

3) The rhamphotheca is finch-like in shape with the tomium entire; nostrils are circular with a slightly swollen rim and placed close to feathers of the lores.

4) The acrotarsium is covered by five large scutes which do not meet behind. The gap along the planta is filled by soft skin covered with small scutes.

5) The hallux in wet-preserved specimens occurs in the normal posterior position but can easily be brought into the pamprodactyl position.

6) Nestling downs are vestigial, being represented only by a few minute rami on the tips of the contour feathers.

7) Garrod (1876e) and Gadow (1895) were mistaken concerning the arrangement of the plantar, or deep flexor, tendons in *Colius*. (Garrod thought that their structure is like that in the Alcedinidae, Coraciidae, Meropidae and Caprimulgidae, and Gadow identified them with his "Type 5" and therefore like *Buceros* and *Cypselus*.) The true condition, according to Pycraft (1907b: 237-38), is as follows: "The flexor longus hallucis never completely fuses with the deeper tendon: the line of junction is always visible. Further, this tendon, the *fl. long. hall.*, splits up into two, one branch going to the hallux and one to D. II. . . , while the *flex. perf. digit.* splits up to serve D.III.IV. This arrangement so far appears to be unique; yet it has probably been derived from an earlier and more primitive condition, shared in common with the Swifts and Humming-birds. . . however, . . . in the Swifts, as in the Colies, . . . the two tendons . . . still shew traces of their originally separate condition."

8) "Besides the Hornbills and the Macrochires, the Colies are . . . the only flying-birds in which the *latissimus dorsi metapatagialis* is absent" (p. 239).

9) The syrinx is tracheo-bronchial.

10) The intestinal tract is uniquely short and wide, lacks caeca and agrees with that of the swifts in being a modification of the "archecentric" caprimulgid type (Mitchell, 1901a).

11) The skeleton of *Colius* presents "many peculiarities which . . . make this group appear more isolated than is really the case; and this is especially true of the skull" (p. 240).

12) The sternum of the colies resembles that of the Capitonidae but they differ in the structure of the keel (p. 246-47).

13) The condyles of the tarso-metatarsus in *Colius* differ from the condition in the swifts, "a fact which is all the more peculiar since both are pamprodactylous" (p. 248).

In his summary (p. 253) Pycraft reviewed the various comparisons and explained, or explained away, the differences between colies and swifts. He decided that "inasmuch as the Colies are undoubtedly related to the *Cypseli*, they are also related, though more remotely, to the *Caprimulgi*, since this last group represents the stock from which the two former have descended."

The colies form a very isolated group, in the opinion of E. Stresemann (1927-34),

who declined to speculate about their affinities. In his linear sequence the colies are given ordinal rank between the Trogones and Macrochires.

Lowe (1948) objected to W. Sclater's (1924) inclusion of the colies in the "Coraciiformes." Lowe reviewed the characters of the colies, with special attention to the patagial muscles and the ectethmoid in both of which the colies differ from "the Coraciiformes proper." He (p. 581) also repeated Garrod's error concerning the lack of an ossified vomer in the colies. Both Pycraft (1907b) and Schoonees (1963) found a vomer. Lowe did not indicate his preferred taxonomic treatment of the colies except to advocate their removal from the Coraciiformes.

The Mallophaga are uninformative concerning the relationships of the colies (Clay, 1950).

Verheyen (1956e, 1961) reviewed the characters of the colies and concluded that their closest relatives are the honeyguides (Indicatoridae), and to a lesser extent the Cuculi. He pointed out a number of similarities between *Colius* and *Indicator*, including the sternum, furcula, coracoid, pelvis, atlas and the "composition numerique du rachis" (p. 6). He also found a number of differences. Verheyen concluded that the separation of the colies and honeyguides was phylogenetically very ancient and that *Colius* should continue to occupy its own order, Coliiformes.

Sibley (1960: 245) found the paper electrophoretic pattern of *Colius* to be "highly distinctive. It is nothing at all like those of the kingfishers, woodpeckers or parrots and not sufficiently similar to those of swifts to form the basis of a decision. The only resemblance is a general similarity to the Passeriformes in the shortness of the profile."

Starck (1960) described the gross and histological structure of the basitemporal articulation of the mandible in *Colius*. He observed that these features differed from those of the skimmers (*Rynchops*) and plovers but did not make any other comparisons.

A study of the cranial morphology of *Colius* was carried out by Schoonees (1963). His purpose in studying the palate was to decide "to which group and variety" of palatal type "as defined respectively by Huxley and Parker, this group belongs" (p. 228). Schoonees reviewed the papers by Huxley (1867), Murie (1872a), Garrod (1876e) and Pycraft (1907b) in relation to palatal structure and noted discrepancies between their descriptions and his own findings. He confirmed the presence of a small vomer and that the palate is "indirectly desmognathous" (see Parker, 1876: 111) at least in one specimen of *Colius colius*. This verified Pycraft's (1907b) description of the palate in *Colius capensis* (= *C. colius*).

There are similarities between the embryology and development of *Colius* and those of the Pici and Cuculi, according to Schifter (1967), but the differences are so great that he decided the colies should be left in their own order.

SUMMARY

The closest relatives of the colies remain in doubt. That they are not passerine, at least under the present definition of that order, is obvious. The parrots, turacos, rollers, swifts, hummingbirds, cuckoos, barbets, honeyguides, woodpeckers, toucans, king-

fishers, hornbills and trogons have been suggested as the relatives of the colies, and most writers have agreed that they are so distinctive that they require isolation in a separate order. Thus, about the only consensus seems to be that an order Coliiformes, placed among the "higher" non-passerines, is currently the appropriate treatment for the group.

THE EGG WHITE PROTEIN EVIDENCE

ORDER COLIIFORMES

FAMILY COLIIDAE, Colies. 3/6, fig. 35.

Species examined: *Colius colius*, *striatus*, *indicus*.

The egg white patterns of the three species of colies are identical. They appear to lack a Component 18, or it may be indistinct and masked by the four conalbumins that migrate 1-2 cm from the origin. Anodal to the conalbumins and migrating partially with them is an indistinct broad band which may be ovomucoid. The broad, diffuse ovalbumin region migrates only about 5 cm from the origin. It seems not to be sharply defined or subdivided, even in fresh material.

The short, simple pattern of *Colius* resembles those of no non-passerines except the swifts. The patterns of the two groups agree in having a weak Component 18 and in the mobilities of the conalbumins, but in the pattern of the swifts the ovalbumin migrates slightly more rapidly and the ovomucoid lies just cathodal to it.

The pattern of *Colius* is passerine in many respects. It is similar to "pattern type A" of Sibley (1970); thus, among the non-oscines, it resembles only *Pitta*. The mobility of the ovalbumin region of *Colius* is greater than that of, for example, the Sylviidae, Muscicapidae, the Paridae, or the nine-primaried oscines, but it is slower than that of the Corvidae. Yet, all of these similarities could be due to electrophoretic coincidence, and the pattern of *Colius* is difficult to evaluate.

CONCLUSIONS

The colies are distinctive and seem to have no obvious ties to other non-passerine groups with the possible exception of the swifts. We suggest that future studies include critical comparisons between these two groups. A possible relationship to the passerines cannot be dismissed, but we are unable to postulate to which family they might be allied.

ORDER TROGONIFORMES

Family Trogonidae, Trogons

Wetmore, 1960

INTRODUCTION

The trogons are a uniform group of approximately 34 species currently divided among eight genera. *Trogon* (14 species), *Pharomachrus* (3), *Euptilotis* (1), *Priotelus* (1) and *Temnotrogon* (1) occur in the Neotropics. *Apaloderma* (2) and *Heterotrogon* (1) are African, and *Harpactes* (11) occurs from India and Ceylon to southeastern China, Indonesia and the Philippines.

Trogons are among the most colorful birds, the males having the breast and abdomen red, pink, orange or yellow, and the long, graduated tail usually black and white. The upperparts of the males of the American and African species are metallic green; all but one of the Asian species (*Harpactes*) have the dorsum brown.

The Trogonidae have a schizognathous palate (Forbes, 1881c) and uniquely "heterodactyl" feet in which digits 1 and 2 are directed backward, 3 and 4 forward. The unique flexor tendons are Gadow's Type 8; the nostrils holorrhinal and impervious; basipterygoid processes present; a large vomer; two deep sternal notches on each side; large aftershaft; only left carotid; pelvic muscles AX (Garrod); eutaxic; 10 primaries; 11-12 secondaries (H. Clark, 1918); 12 rectrices; oil gland nude; large caeca; syrinx tracheo-bronchial; skin thin and delicate; plumage dense, easily detached; bill short, broad basally, culmen decurved and unciniate; maxillary tomium usually serrate; tongue short and triangular or (in *Priotelus*) fairly long and with a bifurcate tip (H. Clark, 1918).

The principal question concerning the trogons is: to which other living group are they most closely related? A large number of families have been suggested as the relatives of the trogons but proof of such relationships remains elusive.

HISTORICAL REVIEW OF THE CLASSIFICATION

The trogons have been placed in the vicinity of the cuckoos, colies, parrots, toucans, puffbirds, jacamars and rollers from Linnaeus (1758) to the present day. For example,

they appear among these groups in the classifications of Brisson (1760), Illiger (1811), Merrem (1813), L'Herminier (1827), Wagler (1827), Nitzsch (1840), G. Gray (1844-49), Cabanis (1847), and Lilljeborg (1866).

The Coccoygomorphae of Huxley (1867) was somewhat of a "catch-all" group. Although Huxley considered this assemblage to occupy the center of the desmognathous birds, most of the characters that he used in defining it are variable and hardly diagnostic. Using characters of the feet he divided the Coccoygomorphae into four groups: (1) Coliidae; (2) Musophagidae, Cuculidae, Bucconidae, Rhamphastidae, Capitonidae, Galbulidae; (3) Alcedinidae, Bucerotidae, Upupidae, Meropidae, Momotidae, Coraciidae; (4) Trogonidae. Huxley's specimen of *Trogon* was imperfect and he thought that the palate was desmognathous. He therefore placed the trogons in the Coccoygomorphae but he believed that they are most closely allied to the Caprimulgidae, apparently because *Trogon* "possesses basipterygoid processes, in which respect it resembles *Caprimulgus*. . ." As Forbes (1881c) later showed, the trogon palate is actually schizognathous. Had Huxley's material been better, he presumably would have placed *Trogon* in his suborder Schizognathae where it probably would have come to rest near the pigeons.

The trogons lack the ambiens and therefore Garrod (1874a) placed them in his Anomologonatae. Since they have a nude oil gland and intestinal caeca he assigned them to his order Passeriformes between the puffbirds and the bee-eaters. In the same group were the passerines, goatsuckers, rollers and motmots.

Garrod (1875: 345) described the deep plantar tendons of *Trogon massena* and *Pharomachrus mocino* as follows:

In these birds the tendon of the *flexor longus hallucis* is situated, as it ought to be, external to the *flexor perforans digitorum*; it also crosses it superficially, opposite about the middle of the tarso-metatarsae [*sic*], sending down a slender vinculum in the normal manner. The peculiarity is in the ultimate destination of the tendons, the *flexor longus hallucis* and the *flexor perforans digitorum* each dividing into two near the metatarso-phalangeal articulation, the two portions of the former tendon running to the hallux and digit 2, the two of the latter to digits 3 and 4 (*vide* fig. 6). This arrangement is not found in any other group of birds, as far as my experience goes.

P. Sclater (1880) attempted to combine the best aspects of past classifications in his system and he used foot structure as the basis for some of his categories. The unique feet of the trogons prompted him to establish a suborder, Heterodactylae, for the trogons in his order Picariae. He placed them between the suborders Anisodactylae (colies, coraciiforms and caprimulgiforms) and Zygodactylae (Galbulidae, Rhamphastidae, Bucconidae, Capitonidae, Indicatoridae). Reichenow (1882) placed the trogons between the Bucconidae and Galbulidae in his order Scansores.

Huxley (1867) had concluded that the trogon palate was desmognathous but Forbes (1881c), working with better material, found it to be schizognathous. Forbes noted (p. 837) that "if Huxley's group of 'Coccoygomorphae' were retained" the trogons would have to be moved "to some other position, presumably in his suborder 'Schizognathae.' But . . . as we now know from Prof. Garrod's investigations, the so-called Coccoygomorphae are an artificial group, made up of at least three very distinct series of birds. Furthermore, the fact that the Trogons are schizognathous, whereas their near allies, such as the Bucconidae, Galbulidae, Coraciidae, *Podargus*, &c., are desmognathous, shows that the structure of the palate has not that unique and peculiar significance that has been claimed for it in the classification of birds."

Stejneger (1885) placed the trogons in his order Picariae as a superfamily be-

tween the superfamilies Picoideae (piciform birds) and Micropodoideae (swifts and hummingbirds). That he was aware that this position was tentative is indicated by his statement (p. 433) that "the trogons are rather peculiar, showing no special relationship to any other group of the present order, a circumstance which explains the fact that by the different systematists they have been associated with nearly all the groups of the Picariae."

In the opinion of Fürbringer (1888), the trogons are an intermediate type between the Coraciiformes and Pico-Passeriformes. Among the former he noted resemblances to the Caprimulgidae, Coraciidae, and Todidae. He was, however, more impressed by the similarities to the latter and gave the trogons a somewhat isolated position as the Trogones, following the Colii in the suborder Pico-Passeriformes, order Coracornithes. The hummingbirds, swifts, passerines and piciforms were included in the same order.

The trogons exhibit no evidence of a close relationship to the hummingbirds or the goatsuckers (Shufeldt, 1889e). Without real evidence from his anatomical studies, Shufeldt suggested that the trogons might have been derived from the cuckoos rather than from "any other with which I am acquainted" (p. 387).

From his study of the patterns of intestinal coiling Gadow (1889: 315) concluded that "the Trogonidae stand on a lower level than the Cypselidae, Trochilidae, and Coliidae, on the same level as the Caprimulgidae and Coraciidae, and connect them all with each other." He pointed out that the trogons possess well-developed caeca of similar structure to those of the Coraciidae, Caprimulgidae, and Strigidae.

Seebohm's (1890a) classification was a curiously anachronistic mixture of past arrangements, with the trogons placed between the hoopoes and the pigeons. This latter alliance was apparently prompted by the schizognathous palate, in spite of Forbes' (1881c) critique. Seebohm (1890b) treated the trogons as a suborder Heterodactyli of his order Pico-Passeres. He underscored the unique arrangement of toes and correlated development of the plantar tendons of trogons. He also noted that "they combine the cranial characters of *Caprimulgus* with the pterylosis of *Motacilla*, and the thigh-muscles and sternum of *Alcedo*. They are schizognathous and holorhinal; and they are the only birds of the Order of Pico-Passeres which permanently retain their basipterygoid processes" (p. 37). In 1895 Seebohm retained the trogons as a distinct order between his Coraciiformes and Piciformes.

Sharpe (1891) believed that the trogons are the "most isolated" of the pico-passerine birds. He put them in a separate order between the suborder Colii of his Coraciiformes and his order Coccoyges.

The trogons possess a simple arrangement of their wing coverts which is most similar to that of the swifts and hummingbirds (Goodchild, 1891).

Gadow (1892) included the suborder Trogones between the Colii and the Coraciae in his order Coraciiformes. The owls, swifts, hummingbirds, goatsuckers, and the coraciiforms were placed in the same order. Gadow (1893) felt that the trogons branched off among ancestral coraciiform birds near the point of division between the Coraciae and the Striges-Caprimulgi. In his linear sequence (p. 301) he placed the Trogones between the Colii and the Pici, the Galbulidae being the adjacent family on the piciform side.

Beddard (1898a) reviewed the anatomical characters of the trogons but made no statement concerning their relationships to other groups except to note that "the very powerful tensor brevis muscle" is similar in certain ways to that of the passerines and that there are also resemblances to the Pici. He placed the Trogones between the Colii and the Coraciae.

The arrangement of intestines in the trogons is derived from a basic "coraciiform-cuculiform metacentre. . . . The Meropidae, the Momotidae, and the Trogones all

retain the metacentric position with extremely little alteration" (Mitchell, 1901a: 257).

Shufeldt (1904b) placed his "supersuborder" Trogoniformes between the Jacamariformes and the Coccoygiformes but did not comment specifically on their resemblances to these or other groups. Reichenow (1913-14) placed the Trogonidae next to the Coliidae in his order Scansores, which also included the Piciformes and Cuculiformes of Wetmore (1960).

Chandler (1916) commented that the structure of the remiges of the trogon *Priotelus temnurus* seems much like that of *Coracias* but that the down feathers of the trogons are most similar to those of the Trochilidae. He made no specific proposals regarding the affinities of the Trogonidae.

H. Clark (1918) examined the pterylosis and other characters of the Cuban trogon (*Priotelus*). Although he presented no conclusions he noted that the "spinal feather tract is quite passerine and those of the ventral surface are nearly as much so" (p. 286). However, the "tracts of the head are entirely separated from those of the lower neck and throat, to a degree and in a manner which I have never seen in any other birds. . . . The secondaries are eleven or twelve in number but one or two of those at the elbow are very small and in examination of a skin, there would seem to be but ten; Nitzsch says there are eight to ten secondaries in the trogons" (p. 287). Clark also found that the tail coverts in *Priotelus* have "the usual passerine arrangement" (p. 288). He confirmed that the palate is schizognathous, as described by Forbes (1881c), and found the tongue to be fairly long and with a bifurcate tip in comparison with previous descriptions of trogon tongues as short and triangular. Clark observed that the large gizzard was full of fruits and the caeca "relatively very long, much longer than in the species of *Trogon* and *Pharomachrus* examined by Garrod" (p. 289).

E. Stresemann (1927-34) concluded that the trogons apparently are without close relationships to the other orders of tropical, arboreal birds ("Baumvögeln"). He gave them ordinal rank between the Upupae (hoopoes, wood-hoopoes, hornbills) and Colii (colies).

Glenny (1943a, 1945c) examined the main arteries near the heart in 13 species of American and African trogons. He found all to have only the left carotid and to exhibit "a high degree of uniformity in the arterial arrangement-pattern . . . in contrast to the . . . pattern-variations observed in the Coraciiformes and Piciformes" (1945: 409).

Lowe (1948) questioned the composition of the Coraciiformes of W. Sclater (1924) and argued that the trogons "cannot be so included." He confirmed that *Harpactes*, like other trogons, is schizognathous and thus all trogons differ in this respect from the desmognathous rollers (*Coracias*) and other coraciiforms of Wetmore (1960). Lowe also laid great stress upon the different form of the ectethmoid in the two groups, and the two carotids in *Coracias* versus only left in the trogons.

Dorst (1950) described the microscopic structure of the feathers in several genera of trogons. He did not comment upon their relationships to other groups other than to make comparisons with the hummingbirds, which indicated differences of, presumably, adaptive rather than taxonomic significance. Pinto (1950) reviewed some of the characters of the trogons but added nothing to the debate concerning their relationships to other groups of birds.

The Mallophaga of trogons are similar to those of the passerines (Clay, 1950).

Mayr and Amadon (1951), without comment, listed the Trogones between the Caprimulgi and the Coraciae.

Verheyen (1956a) reviewed the morphological characters of the trogons and concluded that they share the most similarities with the Caprimulgi and next with the owls. He put the trogons in his order Caprimulgiformes between the Caprimulgi

and the Steatornithes. Verheyen (1960c) proposed an arrangement based, at least in part, upon the number of vertebrae in the six regions of the vertebral column. In this paper he again considered the trogons to be caprimulgiform. The next year (1961) he abruptly changed his mind and gave the trogons subordinal rank in his Coraciiformes next to the swifts.

Sibley (1960) reported that the paper electrophoretic pattern of the egg white proteins of *Apaloderma narina* is similar to that of the passerines in being short and relatively simple. Otherwise there was "little in the egg-white profile to suggest relationships" (p. 246).

Durrer and Villiger (1966) examined the fine structure of the iridescent feathers of five genera of trogons by electron microscopy. They found four different structures within the trogons and essentially identical structural patterns in the iridescent feathers of hummingbirds, *Galbula*, the shining starling (*Lamprotornis*), and the pheasant *Lophophorus*. It was clear that the similarities were due to convergence and would not be trustworthy clues to relationship.

SUMMARY

The consensus is clear; the trogons constitute a distinctive group whose closest relatives are unknown but are to be sought among the "higher" non-passerines and, possibly, the passerines. The colies, goatsuckers, rollers, swifts, cuckoos, jacamars and passerines have been most frequently mentioned as possibly related to the trogons but the conflicting evidence and the uncertain taxonomic value of the utilized characters place all suggestions and "conclusions" in the realm of speculation.

One reason for ambiguity in placing the trogons systematically seems to derive from their possession of heterodactyl feet. This feature makes them "fit" poorly among other higher non-passerines where great emphasis has been laid on the structure of the feet and deep plantar tendons.

Unlike other problem groups the trogons have received little attention from systematists. No comprehensive study of the anatomy of trogons has been undertaken with the purpose of making critical comparisons with all key groups.

THE EGG WHITE PROTEIN EVIDENCE

ORDER TROGONIFORMES

FAMILY TROGONIDAE. Trogons. 1/35, fig. 35.

Species examined: *Apaloderma narina*.

A single pattern of trogon egg white has been available for study. A dense Component 18 migrates 1.5 cm anodally from the origin. The conalbumins, which also stain intensely, are seen between the origin and Component 18. The other main aspect of the pattern is a broad band about 6 cm from the origin. This band clearly is multiple, but the details cannot be made out.

The mobilities and other aspects of the conalbumins and the dense Component 18 are most similar to those of some coraciiform birds (e.g., *Eurystomus*, *Upupa*). The single "ovalbumin" region is reminiscent of the patterns of swifts, colies, and some passerines, but the mobility is faster. The characteristics of this region correspond

best to those of *Upupa* and *Centropus*, but because details are lacking in the pattern of *Apaloderma*, the critical comparisons are difficult to interpret.

The pattern of *Apaloderma* is quite different from those of the Caprimulgiformes or Piciformes.

CONCLUSIONS

The affinities of the trogons remain obscure, but, in our opinion, the Coraciiformes should receive close scrutiny in seeking evidence of relationship. Additional egg white is needed for further biochemical comparisons. The trogons are poorly known in many ways, and we suggest that a thorough anatomical study of them might bring to light new characters of value in assessing their relationships.

ORDER CORACIIFORMES

Suborder Alcedines

Superfamily Alcedinoidea

Family Alcedinidae, Kingfishers

Superfamily Todoidea

Family Todidae, Todies

Superfamily Momotoidea

Family Momotidae, Motmots

Suborder Meropes

Family Meropidae, Bee-eaters

Suborder Coracii

Family Coraciidae, Rollers

Family Brachypteraciidae, Ground-rollers

Family Leptosomatidae, Cuckoo-rollers

Family Upupidae, Hoopoes

Family Phoeniculidae, Wood-hoopoes

Suborder Bucerotes

Family Bucerotidae, Hornbills

Wetmore, 1960

INTRODUCTION

Few orders of birds exhibit such a high degree of heterogeneity as the Coraciiformes as defined by Wetmore (1960). It is difficult to find many characters that apply to all of them and yet the members of this group have been placed together or near to one another in most of the classifications since Linnaeus (1758). The palate is desmognathous, they lack an ambiens and the pelvic muscle formula is AXY (Garrod, 1873d) except in the Alcedinidae, in which it is AX. The feet vary but always have three toes directed forward and a hallux present. Basipterygoid processes are absent or rudimentary; the hypotarsus is complex and the syrinx is tracheo-bronchial or bronchial (*Leptosomus*).

The principal taxonomic questions concerning this assemblage are:

- 1) Are the families included in the Coraciiformes by Wetmore (1960) more closely related to one another than any one of them is to the members of some other order?
- 2) What are the relationships among the groups included in the Coraciiformes?

HISTORICAL REVIEW OF THE CLASSIFICATION

Linnaeus (1758) placed all of the coraciiforms (*sensu* Wetmore) in his order Picae, although not in a single cluster. *Upupa* was placed next to *Certhia* because of the long, slender bill and *Coracias* was next to the starlings and *Oriolus*. However, *Buceros*, *Alcedo*, *Merops* and *Todus* were allied as having "Pedibus gressoriis"; thus the similar foot structure formed an early basis for the group.

In a classification based upon the feet and bill, Illiger (1811) placed *Alcedo* and *Merops* together (Angulirostres); *Upupa* with *Tichodroma* and *Nectarinia* (Tenuirostres); *Buceros* in the Dentirostres and *Coracias* with *Corvus*, *Paradisaea*, etc., in the Dentirostres. All were included in the order Ambulatores.

Temminck (1820-40) adopted a scheme similar to that of Illiger, and L'Herminier (1827) placed the rollers, bee-eaters, kingfishers and hornbills in a linear series with the hoopoes following after the toucans and woodpeckers.

Nitzsch (1840) set up an order Picariae which included, among others, all of the coraciiforms. In his Todidae were *Coracias*, *Momotus*, *Todus* and *Galbula*, followed by the Cuculinae (cuckoos, *Indicator*, *Trogon*), the Picinae (*Bucco*, *Capito*, toucans, woodpeckers), Psittacinae (parrots), Lipoglossae (*Buceros*, *Upupa*, *Alcedo*) and the Amphibolae (turacos, colies, hoatzin). Thus the tendency to place the coraciiforms together received further support although they were placed in two separate groups and mixed in with the piciforms and others.

Based upon external characters, G. Gray's (1844-49) system grouped the rollers, todies, motmots, kingfishers and bee-eaters with the broadbills, trogons, puffbirds and jacamars, *Upupa* with the curve-billed paradiseid *Epimachus*, and the hornbills with the hoatzin, turacos and colies.

Todus was assigned to the Tyrannidae by Cabanis (1847) but the rollers, hoopoes, bee-eaters, kingfishers and hornbills (plus the broadbills and *Podargus*) were brought together in the Coraciidae.

In his review of the nomenclatural history of the wood-hoopoes (*Phoeniculus*), Strickland (1843) concluded that *Irrisor* was the correct name. He compared this group with *Upupa* on the basis of beaks, feet and plumage characters and concluded that the two genera are related and should be placed in two subfamilies within the Upupidae. He was only partially successful in his attempt to determine the nearest allies of the Upupidae for he "conjectured that they are allied in one direction by means of *Epimachus* or *Astrapia* to the Paradiseidae, and in another by *Merops* to the Alcedinidae . . . in a third direction they are perhaps connected through *Lamprotonis* with the Corvidae" (p. 243).

P. Sclater (1865b) reviewed the history of knowledge concerning the cuckoo-roller, *Leptosomus discolor*, and described its pterylosis, skeleton, tongue, and feet. He noted the unusual slitlike nostrils, which are shaped like those of *Eurystomus* but which, in *Leptosomus*, are located near the tip of the bill rather than near the base. *Leptosomus* has 10 primaries, 12 secondaries, 12 rectrices and a large aftershaft on the body feathers. The most remarkable feature of the feathering is the presence of a

large patch of powder down on each side of the rump. Sclater found that the sternum is not especially similar to that of *Coracias* but neither is it "in any respect more like that of the Cuculidae" (p. 161). The feet differ from those of the cuckoos, puffbirds and other zygodactyl groups although the fourth toe tends to extend "laterally, rather more behind than in front." He recommended that *Leptosomus* be removed from the Cuculidae and placed near the Coraciidae in its own family. *Brachypteracias* "may be the missing link which connects *Leptosoma* with the Coraciidae" (p. 163).

Huxley (1867) was possibly the first to bring all members of the group together. His Coccoygomorphae included, in sequence, the Coliidae, Musophagidae, Cuculidae, Bucconidae, Rhamphastidae, Capitonidae, Galbulidae, Alcedinidae, Bucerotidae, Upupidae, Meropidae, Momotidae, Coraciidae and Trogonidae.

The arrangements of Carus (1868-75) and Sundevall (1872) did not keep the coraciiforms together and that of Garrod (1874a) divided them between the orders Piciformes (including Upupidae, Bucerotidae, Alcedinidae) and Passeriformes (including Meropidae, Coraciidae [= Coraciinae], Momotinae, Todinae).

The muscles of the neck, the viscera, oil gland, tongue and orbital region of the skull in *Ceryle torquata stellata*, *Dacelo gigas* and *Alcedo atthis ispida* were studied by Cunningham (1870). In most of these characters the three species differed but *Ceryle* and *Alcedo* were alike in the structure of the tongue and the shape of the lachrymal bone.

In a monograph of the kingfishers Sharpe (1868-71) postulated that the Alcedinidae are related to the Todidae through *Myioceyx*, to the Bucerotidae through *Dacelo* and *Melidora*, and to the Meropidae through *Tanyisiptera*. He recognized the two subfamilies Alcedininae (including *Ceryle*, *Pelargopsis*, *Alcyone*, *Alcedo*, *Corythornis*) and Daceloninae (including the remaining genera).

Todus is closest to the diminutive motmot *Hylomanes momotula* and also closely allied to the kingfishers, according to P. Sclater (1872).

On the basis of osteology Murie (1872b) considered the motmots to be closely related to the todies, next most closely related to the kingfishers and less closely to the rollers. The todies he believed to be closely related to the motmots, next to the kingfishers, then rollers and finally to the bee-eaters.

Murie (1872c) also studied the skeleton of *Todus* and recommended its placement in a separate family, closest to the motmots and kingfishers. Although *Todus* has a desmognathous palate Murie thought that it has many passerine features in its skeleton.

According to Murie (1873: 181) it was Gould who "originally suggested the relationship of the Hoopoes to the Hornbills, an idea which took root and fructified under its foster-parent, Mr. Blyth." Murie reviewed the literature on the hoopoes and hornbills and added "additional data, structural and otherwise" (p. 191) bearing upon the question. He examined the pterylosis, viscera, skeleton, tongue and other characters of *Upupa*, *Phoeniculus (Irrisor)*, *Rhinopomastus* and various other genera that had been considered as possible relatives.

Murie dismissed Sundevall's conjunction of the hoopoes with the larks, and other proposals of their alliance to creepers (*Certhia*), sunbirds (*Nectarinia*), starlings, crows, riflebirds and birds-of-paradise. Neither did he find solid evidence for a relationship between hoopoes and bee-eaters, kingfishers, rollers and motmots although "*Merops* and *Alcedo* offer more than a mere passing likeness" (p. 205). Murie concluded that the hoopoes are most closely related to the hornbills and that the small hornbills (e.g., *Tockus*) show the greatest resemblances to the Upupidae. The Tertiary fossil "*Cryptornis antiquus* (Gervais), . . . discovered in the gypsum near Paris" (p. 206), was suggested as the possible link between *Upupa* and the hornbills. Murie

agreed with "Strickland's juxtaposition of *Upupa* and *Irrisor*" (= *Phoeniculus*) and stated (p. 207) that "the Irrisoridae [= Phoeniculidae] contain two . . . genera, *Irrisor* and *Rhinopomastus* . . ."

In the ground-hornbill (*Bucorvus*) the carotids are reduced to fibrous imperforate cords and their function as blood vessels has been assumed by the enlarged "comes nervi vagi" (Garrod, 1876a; Ottley, 1879).

Garrod (1878a) placed the motmots in his order Piciformes, which included the Bucerotidae, Alcedinidae, Todidae and Capitonidae, as well as the Picidae. Within this assemblage he believed that the todies are the nearest relatives of the motmots. This arrangement was based upon the fact that motmots (except *Momotus*) have a tufted oil gland and lack colic caeca. These characters differentiate them from the Coraciidae, which Garrod placed in the Passeriformes.

The coraciiforms were grouped with the colies, *Podargus*, and *Steatornis* in P. Sclater's (1880) suborder Anisodactylae of his order Picariae. In Stejneger's (1885) arrangement the order Picariae includes eight superfamilies. In the Coracoideae were the caprimulgiforms, Coraciidae and Leptosomatidae; then the Colioideae, followed by the Alcedinoideae (Meropidae, Todiidae, Momotidae, Alcedinidae, Bucerotidae) and the Upupoideae (Upupidae, Irrisoridae [= Phoeniculidae]).

Forbes (1880b) dissected a specimen of the cuckoo-roller, *Leptosomus discolor*, and compared its structure with that of cuckoos, rollers, parrots, etc. The foot structure and the arrangement of the deep plantar tendons is like that in *Coracias*, not as in the cuckoos, parrots, or piciforms. *Leptosomus* agreed with the rollers in pterylosis, lack of an ambiens, and several other characters. However, *Leptosomus* also differs from *Coracias* in syringeal structure and the presence of powder downs. Forbes concluded that the cuckoo-roller is closest to the true rollers but he evaded the question of whether it should be treated as a subfamily, as proposed by Sharpe (1868-71), or a separate family, as suggested by Sclater (1865b).

Forbes (1882c) dissected several specimens of *Todus* and examined almost all of the usual morphological characters. He corrected several of Nitzsch's and Murie's observations and listed 18 points of difference between the todies and the motmots. He was unable to "agree to the proposition that the Todies are more closely related to the Motmots than to any other group" (p. 449) and, instead, concluded "that *Todus* is a much isolated form, with affinities to both the Passeriformes and Piciformes of Garrod" and that it should be placed in "a group *Todiformes*, equivalent to *Passer-*, *Pici-*, and *Cypseliformes*, for the sole reception of the genus *Todus*." Although modified and specialized, this genus "represents more nearly than any other existing form the common stock from which all the living groups of Anomalogonathous birds have been derived" (p. 450).

The osteology of the belted kingfisher (*Ceryle alcyon*) of North America was described by Shufeldt (1884), who also reviewed the classification of the order Picariae, which he considered to be an unnatural group.

"The Bee-eaters must certainly be ranged next to the Rollers, to which they are very closely allied, and they are also nearly allied to the Jacamars, as also, but in a less degree, to the Kingfishers, Motmots, Hoopers [*sic*], and Hornbills" (Dresser, 1884-86: xi.). To support this point of view Dresser quoted at length from Beddard's notes on pterylography, osteology, and myology. In a subsequent monograph of the Coraciidae he (1893) restated his opinion that the rollers are allied to the bee-eaters and jacamars, once again quoting Beddard's notes on anatomy.

It was Fürbringer (1888) who set the pattern for the presently accepted system. His order Coracornithes contained four suborders. In the Halcyoniformes were the kingfishers, hoopoes, hornbills and bee-eaters. The motmots and todies were in an "Intermediate Gens Todi" and the Coraciiformes contained the rollers, cuckoo-rollers,

caprimulgiforms and the owls. The Coccoyiformes contained the cuckoos and turacos, and the Pico-Passeriformes included the Piciformes of Wetmore (1960), the passerines, the Apodiformes, colies and trogons.

The viscera, syrinx and musculature of several species of hornbills were examined by Beddard (1889c). Although the main object of his paper was "to fix some of the generic types" Beddard stated (p. 593) that the only birds to which the hornbills "might be supposed to be allied . . . are the Colies and Caprimulgidae; the presence of the ligament uniting the biceps to the tensor patagii in *Bucorvus* is no doubt the representative of the muscular slip existing in the former groups. . . . *Podargus* has the same great development of muscular fibres in the horizontal septum attached to the gizzard that has been recorded above in the Hornbills."

Seebohm's (1890a-c) classification contained many bits of nonsense due to his attempt to adhere to an arbitrary set of characters. The hoopoes were placed in the order Pico-Passeres while the kingfishers, rollers, hornbills, etc., were allied with the goatsuckers and the swifts in the order Picariae. The New World vultures (*Cathartes*) were assigned to the subclass Coraciiformes, next to the Bucerotes, because of the arrangement of the flexor tendons! In 1895 Seebohm excluded the Cathartidae from his Coraciiformes and transferred the Upupidae to the Cuculiformes, but otherwise his classification remained unchanged.

P. Sclater (1890) noted the presence of the fifth secondary (i.e., eutaxy) in the "Anisodactylous Picarians" and listed *Colius*, *Buceros*, *Upupa*, *Merops*, *Todus*, *Podargus*, *Steatornis* and *Coracias* as being "quintocubital." However, he found "a singular anomaly . . . in the Alcedinidae" in which the fifth secondary is "present in *Alcedo ispida*, *Cittura sanguirensis*, and *Ceryle americana*, but absent in *Halcyon vagans* and *H. chloris*. What is still more remarkable, it seems to be absent in *Ceryle alcyon*, though it is certainly present in a specimen of *C. americana* now before me" (p. 80).

The Coraciiformes of Sharpe (1891) was a large assemblage containing the usual groups as well as the caprimulgiform birds, swifts, hummingbirds, and colies. In his linear list the suborder Leptosomati was next to the Podargi, followed by the suborders Coraciae, Halcyones, Bucerotes, Upupae, Meropes, Momoti and Todi.

Gadow's (1892) Coraciiformes included the owls (Striges); goatsuckers, swifts and hummingbirds (Macrochires); colies (Colii); trogons (Trogones); and the rollers, motmots, kingfishers, bee-eaters, hoopoes and hornbills (Coraciae). His next arrangement (1893) was essentially the same but included the Pici as an additional suborder in the Coraciiformes. The Pici were part of the Passeriformes in his 1892 list.

"The family Alcedinidae shows more structural variation within its own limits than any other family of Picarian Birds." With this introduction Beddard (1896c) examined the pterylosis, wing tendons and other characters of the kingfishers and recorded the diversity that he found in the expansor secundariorum, the fifth secondary, tensor patagii brevis, the biventer link of the cervical musculature and the condition of the uropygial gland. However, in all of the examined species the pelvic muscle formula was AX— and the syrinx was tracheo-bronchial. The great structural variation precluded the "subdivision of the family, at least without further facts. . . ." He pointed out "the somewhat disappointing fact that no particular results seem to be obtainable from a comparison of the quintocubital with the aquintocubital genera" (p. 606).

Beddard (1898a) included the Bucerotidae and the Upupidae (with *Phoeniculus* [*Irrisor*] and *Rhinopomastus*) in his Bucerotes. His Coraciae contained the Coraciidae (with *Leptosomus*, *Brachyteracias*, etc.), Meropidae, Momotidae, Todidae and Galbulidae. The kingfishers were placed in the Alcedines, between the Pici and the Colii. Thus the jacamars (Galbulidae) were placed with the coraciiforms while the

puffbirds (Bucconidae) were allied with the Pici. "The skull of the Galbulidae is very like that of the Bucconidae . . ." (p. 214).

The osteology of *Bucorvus* was studied by Beddard (1901b), who limited his comparisons to other hornbills and made no comments concerning the relationships of the Bucerotidae to other groups.

The anatomy of the kingfishers, and especially the presence (eutaxy) or absence (diastataxy) of the fifth secondary, was investigated by Mitchell (1901c). In the 17 species of kingfishers he examined some were eutaxic, some diastataxic, and some intermediate. He concluded that these conditions, "as in the Columbidae, . . . cannot be regarded as fundamental characters in . . . classification. Both conditions occur, scattered as it were indiscriminately within the confines of the group, and sometimes even within the confines of a genus" (p. 102). In addition, Mitchell examined the myology of a number of kingfishers, seeking correlations between the condition of the fifth secondary and variations in musculature. In the arrangement of the deep plantar tendons there were at least 10 variations. Correlations existed between the tendinous pattern and the condition of the fifth secondary, at least in a general way, and were due to "changes which may be summed up as specialization. There is no *rigid* correlation between the degrees of specialization of different organs in the same species . . . but there is a general correlation, so that if any species be far advanced in one organ it is more likely to be far advanced in other organs . . ." (p. 121).

Regardless of the validity of Mitchell's explanation it seems clear that the condition of the fifth secondary is not a firm basis for the classification of the higher categories.

Fürbringer (1902) modified his earlier (1888) classification of the order Coracornithes by recognizing three suborders: Coccoygiformes (= turacos, cuckoos); Pico-Passeriformes (= Piciformes of Wetmore, 1960; passerines, swifts, hummingbirds, colies, trogons); and Coraciiformes (= Coraciiformes, Caprimulgiformes and Strigiformes of Wetmore, 1960).

The classification of the kingfishers was reviewed by Shufeldt (1903b) and their skeletons compared with those of several other groups. He thought that the kingfishers "are most nearly related to the Galbulidae" (p. 722) but he also found resemblances to the roadrunner (*Geococcyx*: Cuculidae) and to the bee-eaters (Meropidae). Shufeldt (1904b) erected the "supersuborders" Coraciiformes (= Leptosomatidae, Coraciidae) and Halcyoniformes (the remaining coraciiform groups) but did not mention any details concerning relationships.

Chandler (1916) accepted the large order Coraciiformes of Knowlton (1909), which included all non-passerine groups above the Cuculiformes of Wetmore's (1960) list, but he was perplexed in assessing relationships among these groups on the basis of feather structure. He determined that the remiges of *Coracias*, *Momotus*, and *Merops* are most similar to one another, but those of the Alcedinidae differ considerably from this type. *Upupa* and *Irrisor* (= *Phoeniculus*) were similar and could be distinguished from the other coraciiforms. The same was true of the hornbill genera *Anthracoceros*, *Hydrocorax* (= *Buceros*), and *Lophoceros* (= *Tockus*). In the structure of the down, *Coracias*, *Merops*, *Momotus*, and *Phoeniculus* were nearly alike. The down of the kingfishers differed somewhat, but the down barbules of the hornbills have a "peculiar and unusual appearance." Chandler did not speculate on the relationships among the coraciiform groups but merely concluded that "the Coraciidae and near allies, the Striges, Caprimulgi, Bucerotidae and Cypselidae, have types of feathers which are to be regarded as independent offshoots from the main line of evolution" (p. 378).

The purposes of W. D. Miller's (1912) study of the kingfishers were "to establish the proper subfamily divisions of the Alcedinidae" and to determine "the char-

acters and relationships of the three genera currently united under *Ceryle*" (p. 239). He examined skins and skeletons and reviewed the classifications of the kingfishers. He advocated splitting *Ceryle* into three genera (*Ceryle*, *Megaceryle*, *Chloroceryle*) and the recognition of three subfamilies (Cerylinae, Alcedininae, Daceloninae) in the Alcedinidae. Miller (1915) found *Coracias* and *Eurystomus* to be diastataxic, not eutaxic as had been stated by Gadow and Beddard. "*Corapitta* [= *Atelornis*] *pittoides* is apparently eutaxic" and "*Leptosoma* has not been investigated" (p. 131).

W. D. Miller (1920) reviewed the nomenclature and characters of the kingfishers of the subfamily Cerylinae and again recommended the recognition of three genera—*Megaceryle*, *Ceryle* and *Chloroceryle*. He examined the deep plantar tendons in several species and found points of both agreement and disagreement with Mitchell (1901c). Miller used the condition of the fifth secondary as a major character in his key to the genera of Cerylinae, with *Megaceryle* and *Ceryle* being diastataxic and *Chloroceryle* eutaxic. Miller (1924a) recorded the kingfishers as one of the groups containing both eutaxic and diastataxic species; the rollers, including *Atelornis* (*Corapitta*) and *Brachypteracias*, as diastataxic; and the bee-eaters, motmots, todies, hornbills and hoopoes as eutaxic.

Miller (1924a) found only ten primaries (and no remicle) in the hornbills although Gadow had reported eleven. In the Alcedinidae the remicle is present but the covert of the eleventh primary has been lost. The Alcedinidae, Coraciidae and Momotidae have 10 primaries plus the remicle; in the Meropidae, Miller noted "11th very vestigial; 10 in Meropinae." The Todidae, Bucerotidae and Upupae have 10 functional primaries and no remicle. The Momotidae, "except *Momotus*, have normally but ten rectrices. Several exceptions, however, have been noted and evidently the number of tail-feathers in some of the genera at least is an unstable character. The exceptional specimen of *Baryphthengus ruficapillus* . . . had six rectrices on one side of the tail (the other side being imperfect). A skin of *B. (Urospatha) martii semirufa* . . . has six rectrices on one side, five on the other . . . in *Eumomota superciliaris* also the number varies. Of twenty-four skins . . . , twenty-two have ten rectrices, one has eleven . . . and one has twelve" (p. 319–20).

Miller (1924b) found the aftershaft present in some kingfishers, absent in others and absent in *Upupa* but present in *Phoeniculus*. It is also absent in the hornbills but present in the other coraciiforms. The presence of an aftershaft is "unquestionably a primitive character" and its reduction or loss is a sign of specialization, according to Miller. An aftershaft is absent in the hornbills and hoopoes among others.

Friedmann (1930) drew attention to the variations in the caudal molt of certain coraciiforms, colies and piciforms. The kingfishers apparently have a centrifugal tail molt. The Phoeniculidae seem to have the condition reported in woodpeckers, i.e., the "tail molt is centrifugal beginning with the next to the middle pair and proceeding outward, the middle pair being shed after the fourth pair . . ." (p. 4). In the one bee-eater available the tail molt was irregular and in hornbills the females drop all of the rectrices simultaneously while confined in the nest chamber. In male hornbills of some species the tail molt is regularly centrifugal, in others somewhat irregularly so. As noted by Wetmore (1914) the tail molt in *Rhinoplax vigil* is exceptional in that only one feather of the central pair is developed at one time.

Lemmrich (1931) found essentially identical arrangements and numbers of sclerotic ring plates in *Coracias*, *Alcedo*, *Upupa*, *Picus* and *Dendrocopos*. *Cuculus* and *Psittacus* differ but slightly from the coraciiforms and piciforms in this character.

E. Stresemann's (1927–34) classification, which was repeated unchanged in 1959, recognized six orders for the birds of Wetmore's (1960) order Coraciiformes. Stresemann (1959: 275) preferred "a system that is as realistic as possible, a system in which no room is given to phylogenetic speculations, and in which the gaps in our

knowledge are frankly admitted. If one follows these guiding principles one is forced to recognize a greater number of . . . orders . . . than accepted by Wetmore—indeed even more than I admitted in 1934.” But Stresemann noted (p. 270) that his system “does not differ in essence from those which Wetmore (1951) and Mayr and Amadon (1951) have recommended” since “all are based on Fürbringer and Gadow.” Although Stresemann did not place the coraciiforms in a single order his comments upon their relationships amount to the same thing. The classification (1927–34) and our translation of his comments are presented below.

Order Coraciae—Rollers (Racken)

Family Coraciidae, True Rollers (Echte Racken)

Family Leptosomatidae, Cuckoo-rollers (Kurols)

Family Brachypteraciidae, Ground-rollers (Erdracken)

Place in the system: Fürbringer was inclined to unite the Coraciae and Caprimulgi; other authors, perhaps more correctly, place the Halcyones as the closest relatives.

Order Halcyones—Kingfishers (Eisvögel)

Place in the system: obviously most nearly related to the Meropes, Coraciae and Momoti.

Order Meropes—Bee-eaters (Bienenfresser)

Place in the system: probably related to the Coraciae and Halcyones, perhaps also allied to the Upupae.

Order Momoti—Motmots (Sägeracken)

Place in the system: closest relatives are the Halcyones, Coraciae and Todi.

Order Todi—Todies (Todis)

Place in the system: equally related to the Halcyones and Momoti.

Order Upupae—Hoopoes (Hopfartige)

Family Upupidae, Hoopoes and Wood-hoopoes (Hopfe)

Family Bucerotidae, Hornbills (Nashornvögel)

Place in the system: Fürbringer maintained the Meropes and Halcyones as the nearest relatives of the Upupae and also it seemed to him that there is a relationship with the Passeres.

Lowe (1946: 119) listed 22 characters of *Upupa epops* and noted that the hoopoe “in some respects, especially as regards the palatal region . . . is characteristically Coraciiform; in others typically Passerine and in others Picine. . . . In the Coraciiforms the presence of an Expansor secundariorum muscle is invariable. It is absent in *Upupa* and there are other characters which point to the Pici and Passeres.”

As a tentative arrangement Lowe favored placing the Pici as a suborder of the Passeriformes. The Pici would contain the families Picidae, Indicatoridae, Capitonidae, Rhamphastidae and Upupidae.

Lowe (1948: 572) disagreed with W. Sclater's (1924) definition of the Coraciiformes. “. . . The Coraciiformes have for many years been loaded with a heterogeneous collection of forms which custom has blindly accepted.” He objected primarily to the inclusion of “the Swifts and Humming Birds, to say nothing of the Colies and the Hoopoes.” Lowe was willing to admit the rollers (*Coracias*) and “the following outlying genera, viz. *Eurystomus*, *Brachypteracias*, *Uratelornis*, *Atelornis*, *Geobiastes* and *Leptosomus*” and possibly the Alcedinidae, Meropidae and Momotidae, but “it is certain that the Striges, the Bucerotidae, the Upupidae . . . , the Cypseli, the Coliidae . . . and the Trogonidae . . . cannot be so included” (p. 574).

Lowe advocated (p. 578) a separate order for the hornbills because of “the peculiar structure of the bill and the universal form of the latissimus dorsi muscle”

as well as several additional characters which "prove their complete isolation from the Coraciiformes." The hoopoes are "nearly Passerine, and in any case cannot be associated with the Coraciiformes" (p. 580). Lowe agreed with Forbes (1882b) that *Todus* is an isolated form "with affinities to both the Passeriformes and Piciformes of Garrod" and he advocated the establishment of "a group Todiformes equivalent to Passeri, Pici and Cypseliformes for the sole reception of the genus *Todus*, which is Forbes' summing-up, and with which I agree" (p. 582). Thus the Coraciiformes according to Lowe (1948) would include only the Coraciidae, Brachypteraciidae, Leptosomatidae and, possibly, the Alcedinidae, Meropidae and Momotidae.

The evidence from the Mallophaga which bears on the relationships of the Coraciiformes was reviewed by Clay (1950). The Momotidae, Meropidae, Coraciidae, and Upupidae are parasitized by some genera which are shared with or closely related to those on the passerines. The Coraciidae and Meropidae share members of the genus *Meromenopon*. *Hopkinsiella*, which is found on the Phoeniculidae, seems to be related to *Upupicola* on the Upupidae. The mallophagan faunas of the Alcedinidae and Bucerotidae are distinctive and cast no light on relationships.

Delacour (1951b) considered the reduction in the number of toes in some kingfishers to be unimportant as a basis for the classification of the small kingfishers of the subfamily Alcedininae. He advised that "the number of toes be disregarded" and that the species be assigned to *Alcedo* and *Ceyx* according to other characters, including their habitat and coloration.

The Coraciiformes were reviewed by Verheyen (1955d), who examined the characters, especially of the skeletons, of the groups included in the order by Wetmore (1934). Verheyen presented his conclusions in a new classification which utilized two orders—Upupiformes (Upupidae, Phoeniculidae, Bucerotidae) and Coraciiformes (Leptosomatidae, Coraciidae, Meropidae, Momotidae, Alcedinidae, Todidae)—to contain the birds in Wetmore's Coraciiformes. Verheyen (1961) reduced these two orders to subordinal rank and expanded the Coraciiformes to include the suborders Trochili, Apodi, and Trogones.

The paper electrophoretic patterns of the egg white proteins provided Sibley (1960) with evidence that the bee-eaters, motmots and kingfishers are related to one another but that "the only available roller (*Eurystomus*) seems to have nothing in common with these others but is strikingly similar to that of the parrot *Psephotus varius*" (p. 243). This similarity was ascribed to coincidence, not to close relationship.

The structures of the casque and bill in the helmeted hornbill, *Rhinoplax vigil*, were studied by Manger Cats-Kuenen (1961) and compared with other hornbills. The functions of the casque in the Bucerotidae in general are primarily as a signal character, "to overawe assailants and congeners," and "the larger casques probably serve as a soundboard" (p. 46). In *Rhinoplax* "the heavily reinforced casque with its thick rostral horn layer . . . will be able, like the heavy head of a hammer, to add force to the blows of the smaller, short, straight and less imposing bill. The casque itself, built to intercept blows, will have been modified to serve . . . as a hammer in the acquisition of food, as a shield for the defense against enemies . . . and as a 'trowel' for building the wall of the nest" (p. 46).

V. and E. Stresemann (1961b) separated the Alcedinidae into three subfamilies on the basis of the molt pattern of the primaries. The Daceloninae (including *Pelargopsis*) follow the descending mode, beginning with the first primary. A descending pattern is also followed by the Alcedininae, but molt begins at two foci, represented by the first and seventh primaries. In the Cerylinae the primary molt is more or less irregular and never follows the descending pattern. These three groups "agree exactly with the three subfamilies . . . as classified in 1912 by W. DeW. Miller, who based his

arguments on morphological evidence" (p. 445). The Stresemanns also presented a historical review of the classification of the kingfishers.

Forbes-Watson (1967) reported on the first known nest of the cuckoo-roller (*Leptosomus discolor*), which he discovered on Mayotte Island in the Comoros. He presented data on various aspects of the nest, young, food and behavior. Using only the evidence afforded by his observations Forbes-Watson (p. 430) suggested that "the Leptosomatidae would not seem to be particularly closely-related to the Coraciidae. . . ." The remnants of copious white down on the young cuckoo-rollers suggested a possible relationship to the Upupidae, which is the only family of the Coraciiformes which "has down, and that is scanty. . . . The tinted, not pure white, eggs and smelly nest also remind one of the Upupidae and also of the Phoeniculidae."

Cracraft (1971) reviewed the classification of the rollers and presented new data on their osteology. He proposed a classification of the suborder Coracii as follows:

Superfamily Coracioidea
 Family Coraciidae
 Family Brachypteraciidae
 Superfamily Leptosomatoidea
 Family Leptosomatidae

SUMMARY

The alliance of the groups currently placed together as the Coraciiformes (Wetmore, 1960) or Coraciae (Mayr and Amadon, 1951) was fixed by the decisions of Fürbringer (1888) and Gadow (1892, 1893). The desmognathous palate and foot structure are apparently the most important characters uniting the group although the subgroups have additional characters in common.

Many authors have placed the todies, motmots and bee-eaters together, usually with the kingfishers nearby. The kingfishers and jacamars have sometimes been allied because they share similar palates, paired carotids and pelvic musculature but the differences in foot structure and flexor tendon arrangement have taken precedence and the jacamars have nearly always been placed with the Piciformes. The hoopoe-hornbill relationship has long been accepted and seems to be based on solid evidence.

The alliance of the Coraciidae, Brachypteraciidae and Leptosomatidae also appears to be well founded but whether or not these three groups of rollers are actually closely related to the other coraciiform groups seems less assured.

During the past century there has been no serious challenge to the larger alliance of coraciiform and piciform birds. The remaining questions concern the validity of the characters which have been used as the basis for the classifications currently in use.

THE EGG WHITE PROTEIN EVIDENCE

ORDER CORACIIFORMES

FAMILY ALCEDINIDAE, Kingfishers, 8/87, fig. 35.

Species examined: *Ceryx alcyon*; *Chloroceryle americana*; *Alcedo atthis*; *Ceyx azureus*; *Dacelo novaeguineae*; *Halcyon smyrnensis*, *leucocephala*, *pyrrhopygia*.

FAMILY TODIDAE, Todies, 1/5, fig. 36.

Species examined: *Todus mexicanus*.

FAMILY MOMOTIDAE, Motmots. 2/8, fig. 36.

Species examined: *Eumomota superciliosa*; *Momotus mexicanus*.

FAMILY MEROPIDAE, Bee-eaters. 9/25, fig. 36.

Species examined: *Melittophagus bullockoides*, *pusillus*; *Merops leschenaulti*, *apiaster*, *superciliosus*, *viridis*, *malimbicus*, *nubicus*, *ornatus*.

FAMILY CORACIIDAE, Rollers. 3/11, fig. 36.

Species examined: *Coracias garrulus*, *spatulata*; *Eurystomus orientalis*.

FAMILY BRACHYTERACIIDAE, Ground-rollers. 0/5.

FAMILY LEPTOSOMATIDAE, Cuckoo-roller. 0/1.

FAMILY UPUPIDAE, Hoopoe. 1/1, fig. 36.

Species examined: *Upupa epops*.

FAMILY PHOENICULIDAE, Wood-hoopoes. 2/6, fig. 36.

Species examined: *Phoeniculus purpureus*; *Rhinopomastus cyanomelas*.

FAMILY BUCEROTIDAE, Hornbills. 2/45, fig. 37.

Species examined: *Tockus flavirostris*; *Bucorvus leadbeateri*.

The egg white patterns of the Coraciiformes are heterogeneous; no two families share the same pattern. The least complicated pattern is that of the Alcedinidae. The conalbumins migrate anodally just off the origin. They are densely stained and obscure Component 18. The next feature of the pattern is a small, well-defined band at about 4 cm. A similar band occurs also in the patterns of the Todidae, Meropidae, and Momotidae. There is a single ovalbumin, which moves more than 7 cm from the origin, and anodal to it are two or three prealbumins. The prealbumins, however, are indistinct in most patterns. The pattern of *Todus* is most like that of the kingfishers but it differs in having a slower ovalbumin.

The patterns of the Momotidae resemble those of the kingfishers in several respects, but they possess a broad ovomucoid which moves 6–7 cm from the origin. The ovalbumin is a smaller band than the ovomucoid and migrates more slowly than the ovalbumin of the kingfishers.

In the patterns of the Meropidae the ovalbumin migrates faster than that of the kingfishers, and the ovomucoid appears as a dense band immediately cathodal to the ovalbumin.

In the patterns of the Coraciidae the conalbumins migrate anodal to Component 18. There is a broad, dense ovomucoid region at about 6 cm from the origin and it is subdivided into several bands. The ovalbumin consists of at least two bands in *Coracias spatulata*, but they are not well defined and stain less intensely than the ovomucoid.

The conalbumins in the pattern of *Upupa epops* have a mobility similar to those of the kingfishers and bee-eaters. About 4 cm from the origin there are three or four pale, indistinct bands. Between 6–7 cm is a broad band which may represent either the ovomucoid or ovalbumin or both. Anodal to this are two or three lighter "prealbumins."

The patterns of *Phoeniculus* and *Rhinopomastus* are similar and somewhat resemble that of *Upupa*. They have a component at about 4 cm from the origin, but it appears as a single densely staining band. The "ovalbumin" migrates faster than that of *Upupa*, and no prealbumins are observable.

The pattern of the hornbill *Tockus* is like those of the Phoeniculidae, but the middle component moves about 5 cm from the origin. The pattern of *Bucorvus leadbeateri* differs from that of *Tockus* in having cathodally migrating conalbumins, a broad, indistinct band beginning at about 3 cm from the origin, and two well-defined components in the ovomucoid region. The significance of the differences between the patterns of *Tockus* and *Bucorvus* is not known. Patterns from additional genera of

hornbills may well bridge the gap. The patterns of the Phoeniculidae and Bucerotidae possess rapidly migrating ovalbumins which move over 7 cm in starch gel. In this respect they are like the ovalbumins of the Alcedinidae and Meropidae.

Because of the heterogeneity of the coraciiform egg-white patterns it is difficult to suggest groupings within the order. The patterns of the Alcedinidae, Todidae, Momotidae, and Meropidae share a broad Component 18 and a dense conalbumin region of similar mobility. They all have a small but distinct band at about 4 cm from the origin, but they differ in the ovalbumin and ovomucoid regions.

The Phoeniculidae share many features of their egg white pattern with the Bucerotidae, but the pattern of *Upupa* is unlike those of either family. The patterns of *Upupa* and of the Coraciidae do not resemble each other or those of the other coraciiform birds.

It is difficult also to find strong resemblances between the patterns of a coraciiform group and those of other non-passerines. They show little similarity to the patterns of the Strigiformes, Caprimulgiformes, or Apodiformes. A vague resemblance is noted between the patterns of some coraciiforms and some cuculiforms (e.g., *Upupa* and *Clamator*), but these may be due to electrophoretic coincidence. Some similarity to the pattern of the trogon *Apaloderma* has previously been noted. There is a striking likeness in the patterns of some coraciiforms and some piciforms, notably between the kingfishers and jacamars. This is discussed in more detail in the Pici-formes section, below.

CONCLUSIONS

The relationships of the coraciiform birds remain imperfectly known. We resist the temptation to split the order because no compelling evidence exists to ally any group of the Coraciiformes more closely to a non-coraciiform than to other members of the Coraciiformes. Our study seems to support a distinct, but rather distant, alliance among the Alcedinidae, Todidae, Momotidae, and Meropidae. We suggest that among these groups the todies are more closely related to the kingfishers than they are to the motmots. Our data also suggest that the possibility of a relationship between the Phoeniculidae and Bucerotidae may profitably be investigated, but we cannot support or deny a close relationship between *Upupa* and the Phoeniculidae. Similarly, the affinities of the Coraciidae to other members of the order are uncertain. The heterogeneity of the order with respect to anatomical characters is matched by the variation in their egg white protein patterns. Clearly the Coraciiformes require further study at all levels.

ORDER PICIFORMES

Suborder Galbulae

Superfamily Galbuloidea

Family Galbulidae, Jacamars

Family Bucconidae, Puffbirds

Superfamily Capitonoidea

Family Capitonidae, Barbets

Family Indicatoridae, Honeyguides

Superfamily Ramphastoidea

Family Ramphastidae, Toucans

Suborder Pici

Family Picidae, Woodpeckers, Piculets

Wetmore, 1960

INTRODUCTION

The Piciformes are zygodactyl birds with flexor tendons of a unique type (Type 6 of Garrod, 1875) in which a vinculum is present but the flexor digitorum supplies only digit III, the other toes being supplied by the trifurcate flexor hallucis. They share some characters with the Passeriformes, others with the Cuculiformes and Coraciiformes.

The Galbulae are desmognathous or aegithognathous, have an AX or AXY pelvic muscle formula (Garrod, 1873d, 1874a) and a normal tongue. The Pici have a saurognathous (or aegitho-schizognathous) palate, pelvic muscle formula AX, an extensile tongue and (except *Jynx*) a chisellike bill.

The principal taxonomic questions concerning the piciforms are:

- 1) Are the Piciformes a natural group of families more closely related to one another than any one is to the members of some other order?
- 2) To what other orders are the Piciformes most closely related?

HISTORICAL REVIEW OF THE CLASSIFICATION

Under various names, and with slightly varying content, the piciform birds were grouped together in most of the early classifications. The Picae of Linnaeus (1758) included most of the piciforms recognized today. The Picae of Moehring (1752) included some passerines, *Cuculus*, *Coracias*, *Merops*, *Upupa*, *Picus* and several other genera. In his Scansores Illiger (1811) placed the parrots, cuckoos, trogons, puffbirds, jacamars, toucans and woodpeckers. The Tribe Zygodactyli of Vieillot (1816) comprised the cuckoos, woodpeckers and parrots. Thus, from the earliest period the foot structure was the main character utilized in the classification of these groups.

Nitzsch (1840) was possibly the first to bring all of the piciforms together in a single order. His Picariae included several subgroups, among them the Todidae (*Coracias*, *Momotus*, *Todus*, *Galbula*), the Cuculinae (*Cuculus*, *Indicator*, *Trogon*), and the Picinae (*Bucco*, *Capito*, Ramphastidae, Picidae).

G. Gray (1844-49) distributed the piciforms between two of his orders but Lilljeborg (1866), who depended mainly upon beak and foot structure, placed all of the Zygodactyli together, as had Vieillot (1816).

Huxley (1867) recognized that the palate of woodpeckers represented a condition intermediate between desmognathism and aegithognathism. This type of palate was termed saurognathous by Parker (1875b). Huxley placed the Galbulidae, Ramphastidae, Bucconidae, and Capitonidae with the cuculiform birds in his Coccoyomorphae. He erected a separate group for the woodpeckers, the Celeomorphae, which he thought to be intermediate between the Coccoyomorphae and the Aegithognathae (= apodiform, caprimulgiform, and passeriform birds).

P. Sclater (1870) was the first to dissect a specimen of *Indicator* which, by most previous authors, had been placed with the cuckoos. He was aware of Blyth's (1842) opinion that the honeyguides are related to the woodpeckers. Sclater examined the tongue, sternum, pectoral girdle, skull, pterylosis and digestive tract of *Indicator*. He concluded (p. 180) that it is not a member of either the Cuculidae or Picidae but required separation in its own family "best placed in the second section of the Coccoyomorphae, as arranged by Prof. Huxley . . . next to the Capitonidae." This treatment put the honeyguides in the same position they hold in Wetmore's (1960) classification.

Marshall and Marshall (1871) defined an order Fissirostres for arboreal birds which use their wings in pursuit of food and whose feet are adapted only for perching. The constituent groups were the caprimulgiforms, trogons, and puffbirds. Their order Scansores was composed of arboreal birds which use their feet in pursuit of food and in which the outer toe is "versatile" or "turned completely backwards." This order included the toucans, barbets, cuckoos, and turacos. In the Marshalls' opinion, the nearest relatives of the barbets are the toucans and honeyguides. The barbets also approach the woodpeckers (e.g., *Picumnus*) through *Barbatula* (= *Pogoniulus*) and the cuckoos (e.g., *Clamator*) through *Trachyphonus*.

In Garrod's (1873d, 1874a) system the order Piciformes included the Picidae, Ramphastidae and Capitonidae but the Bucconidae and Galbulidae were placed in the Passeriformes.

Parker (1875b) studied the morphology of the skull in woodpeckers and wry-necks and commented upon the palatal structure of the group. He noted (p. 2) Huxley's (1867) description of the palate and proposed that the group be called the Saurognathae because the palatal structure is like that of "early embryos of the Passerinae, . . . their palatal region arrested at a most simple and Lacertian stage." Parker concluded (p. 20): "The 'Celeomorphae' of Huxley form a most natural and well-defined group . . . equal, zoologically, to the Pigeons or the Parrots." The palate of *Picumnus* agrees "with that of the last of the Rhynchosaurian Lizards (namely

Hatteria). . . . In the *low* South-American Passerinae, the 'Formicariidae' and the 'Cotingidae,' the essentially Reptilian face shows itself most clearly." The principal character of "the 'Celeomorphae' is the want of fusion of the parts of the palate at the mid line."

The anatomy of a honeyguide (*Indicator*) was also examined by Garrod (1878c), who noted the earlier conclusions of Blyth (1840, 1842), P. Sclater (1870) and Blanford (1870), all of whom considered the honeyguides to be piciform rather than cuculiform. Garrod (p. 931) reaffirmed his confidence in the correlation between the condition of the dorsal pteryla and the presence (homalognatous) or absence (anomalognatous) of the ambiens muscle.

When the dorsal tract develops a fork *between* the shoulder-blades a bird is homalognatous; when the tract runs on unenlarged to near the lower ends of the scapulae, then it is anomalognatous. Again, among the Anomalognatae, when the pectoral tract bifurcates into an outer and an inner branch just after commencing on the chest, then the bird is one of the Piciforms, and has a tufted oil-gland; when the pectoral tract does not bifurcate at all, or only at the lower end of its pectoral portion but is only increased in breadth instead, then the bird is Passeriform, and has a naked oil-gland. Exceptions to these rules scarcely exist.

By these criteria, *Indicator* was declared to be piciform, not cuculiform. In addition, Garrod noted that the palate is "but little different from that of the Capitonidae." The feather tracts of *Indicator* are similar to those of the Picidae, Capitonidae and Ramphastidae and its soft-part anatomy, carotids, deep plantar tendons, pelvic muscles and other characters are also similar to these families and differ from those of the cuckoos. Garrod (p. 935) proposed that the suborder Pici should contain two families, Picidae and Capitonidae, the latter to include the subfamilies Indicatorinae, Capitoninae, and Ramphastinae.

The order Picariae of P. Sclater (1880) encompassed the same birds that Wetmore (1960) had placed in seven orders: Cuculiformes, Apodiformes, Caprimulgi-formes, Coliiformes, Trogoniformes, Coraciiformes and Piciformes. The Pici (Picidae) were placed some distance from the Zygodactylae (Galbulidae, Bucconidae, Ramphastidae, Capitonidae, Indicatoridae). In a monograph of the jacamars and puff-birds Sclater (1882) expressed his conviction that these two families are more closely related to each other than either is to any other piciform group. In the introduction to this volume Sclater quoted Forbes as believing that the Galbulidae and Bucconidae have close affinities with the Meropidae, Coraciidae, and *Leptosomus*.

Forbes (1882a) found a long "intestini-form" gall bladder in a number of species of toucans and barbets. A similar gall bladder is present in woodpeckers. The condition in *Indicator* was unknown to Forbes. He also pointed out the exceptionally large deltoid muscle common to the Picidae, *Indicator*, toucans, and barbets (also in the passerines, some pigeons and *Cariama*). The presence of a sesamoid bone, the "scapula accessoria," was noted in the Pici and in the passerines. Forbes concluded (p. 96) that these additional points of resemblance between woodpeckers and barbets made their relationship "even more certain than before." The cranial differences between the two groups indicated to him that the structure of the skull is not "a certain, or even sufficient, index to their systematic classification."

An order Picariae was also used by Stejneger (1885). It included the same birds as in Sclater's (1880) Picariae but the Piciformes (Wetmore, 1960) were together in the superfamily Picoideae.

Fürbringer (1888) set up the order Coracornithes to encompass the "higher" non-passerines and passerines. The suborder Pico-Passeriformes included the Capiton-

idae, Ramphastidae, Indicatoridae, Picidae, the passerines, Apodiformes, colies and trogons. The Galbulae were placed in an "Intermediate Gens" between the Coccygiformes (Musophagidae, Cuculidae) and the Capitonidae. Thus all of the Piciformes were together and in essentially the same sequence currently used.

The pterylosis of certain woodpeckers was reviewed by Shufeldt (1888e), who described and figured the feather tracts of *Dendrocopos villosus* and *Sphyrapicus varius* and compared them with *Colaptes*.

Shufeldt (1891d) challenged the interpretations of the palatal structure of woodpeckers proposed by Huxley, Parker, and Garrod. He denied any especially reptilian arrangement upon which the "saurognathous" condition was based and, instead, insisted that specialization could account for some of the characters and the errors of his predecessors for others. Shufeldt summarized the "chief osteological characters of the North-American Pici" (p. 126) and "the probable position of the Pici in the System" (p. 128). In his opinion, the woodpeckers are more nearly allied to the passerines than to any other living group.

Within his large pico-passerine order Seebohm (1890b) erected the suborder Scansores for the piciform birds. His diagnosis of the group was based mainly on the deep plantar tendons. He found resemblances among the Scansores, trogons, Upupae, and the passerines. In 1895 Seebohm returned to a more conventional arrangement, recognizing an order Piciformes with the usual groups, but merging the Bucconidae into the Galbulidae and the Indicatoridae into the Capitonidae. This was the same arrangement as that of Gadow (1893).

Sharpe (1891) placed the piciform birds in a separate order, the Scansores, between the Psittaciformes and Passeriformes and recognized suborders for all the major groups. He thought that the woodpeckers, barbets, toucans, and honeyguides are closely related to one another but suggested that the Galbulidae and Bucconidae may not be closely allied.

The Passeriformes of Gadow (1892) included two suborders, Pici and Passeres. The Pici contained the same birds as in Wetmore's (1960) Piciformes. Gadow (p. 234) found that of his 40 characters, 29 were held in common between the Pici and the Psittaci but he thought that the 11 differences were more important than the 29 similarities. He concluded that "the Pici are an offshoot" of the Coraciiformes and that "the resemblances between the Pici and Psittaci have therefore chiefly to be looked upon as convergent analogies."

Gadow (1893) removed the piciform birds from the Passeriformes and placed them in his large order Coraciiformes. He believed that the nearest relatives of the Pici were the Coraciae, especially the Meropidae and Alcedinidae.

Beddard (1896b) called attention to certain errors in Nitzsch's (1840) drawings of the feather tracts in the barbets and toucans and, from his own studies, concluded that these two groups are similar to one another and to the woodpeckers in their pterylography. Beddard also commented upon variations in the feather tracts of barbets associated with generic limits and differences between New World and Old World forms.

Shufeldt (1904b) recognized the adjacent "supersuborders" Picariformes (Capitonidae, Ramphastidae, Indicatoridae) and Piciformes (Picidae). He combined the jacamars and puffbirds into the Jacamariformes, which are between the hummingbirds and trogons in his linear sequence. As is the case throughout his paper Shufeldt did not provide evidence for his interesting proposals.

The Capitonidae, Rhamphastidae, and Picidae share characteristics of their contour feathers that are intermediate between those of the Coraciae and those of the Passeres (Chandler, 1916). *Jacamerops*, a galbulid, seemed to Chandler to be

most like *Coracias*, but in the puffbird *Malacoptila* the barbules are of "typical passerine type." In the structure of the down the Galbulidae and Bucconidae are most like the Coraciidae, and the Capitonidae, Rhamphastidae, and Picidae resemble the passerines. Chandler concluded that "the Trochilidae and the suborder Pici, with the exception of the Galbulidae, show such striking likenesses to the Passeriformes that it is difficult to deny their closer alliance to that group than to the Coraciiformes" (p. 379).

W. D. Miller (1919) confirmed the observations of Garrod (1875) on the deep plantar tendons in the piciforms. He found that the puffbirds and jacamars have the "antiopelmous" arrangement (Garrod's Type 6) as do the woodpeckers, toucans and barbets. Miller cited Stejneger's statement that the honeyguides are antiopelmous, although Miller did not know Stejneger's authority. (Presumably it was Garrod, 1878c; see above). Miller assumed that the wrynecks and piculets are also antiopelmous. He therefore concluded that the birds having zygodactyl, antiopelmous feet form "a natural group, an order or suborder." In addition, these birds lack the ambiens. The other zygodactyl groups, namely, the parrots and cuckoos, have "desmopelmous" tendons (Garrod's Type 1) and an ambiens muscle.

E. Stresemann (1927-34) placed the usual groups in his order Pici and believed them to be most closely related to the "primitive" passerines.

The pterylography of 23 species or subspecies of North American woodpeckers was scrutinized by Burt (1929), who determined that they are essentially uniform. Only *Sphyrapicus* was distinguishable from the other nine genera examined.

In his study of the adaptive modifications in the woodpeckers Burt (1930) reported correlations between morphological characters and habits. He proposed a division of the Picidae into two groups "according to whether or not the accessory semitendinosus muscle is present" and "by the type of skull, that is, whether the frontals are folded or not." One group includes "*Picooides*, *Dryobates*, *Xenopicus*, and *Sphyrapicus*. The other . . . less specialized for arboreal life . . . represented . . . by *Ceophloeus*, *Centurus*, *Balanosphyra*, *Melanerpes*, *Asyndesmus*, and *Colaptes*" (p. 522).

The sclerotic rings of the eyes in woodpeckers are most similar in number of plates and their arrangement to those of *Coracias*, *Alcedo* and *Upupa*. They differ slightly from the conditions in *Cuculus*, some parrots and many passerines (Lemmerich, 1931).

The functional anatomy of the foot in birds with pamprodactyl, heterodactyl and zygodactyl feet was studied by G. Steinbacher (1935). He examined material from all of the piciform families of Wetmore (1960) but did not make comparisons with the coraciiforms, except *Leptosomus*. In this extensive and important study Steinbacher found four basic types of zygodactyl feet in birds, characterized by the "Cuculoidea, die Galbuloidea, die Picoidea und die Psittaci" (p. 277). He considered the cuckoo type to be the most primitive and the woodpecker the most highly specialized. The type of foot in the Galbuloidea was thought to be intermediate between the cuculine and picine structures. Steinbacher concluded that the differences among the various types of foot structures in these groups of birds cannot be explained on purely functional grounds and that they are therefore of great value in systematics.

Krassovsky (1936) gave particular attention to the functional aspects of the palate and other portions of the skull in woodpeckers but was not concerned with their relationships to other groups.

J. Steinbacher (1937) carried out an extensive study of the skeleton, musculature, digestive system, syrinx, pterylography and molt in the jacamars and puffbirds. He compared them almost exclusively with the piciforms, namely, the Picidae, Capiton-

idae and Ramphastidae. Some comparisons were made with the Coraciidae but not with the Alcedinidae or Meropidae. He concluded that the Galbulidae and Bucconidae are closely related to one another and to the Picidae and Capitonidae.

The Capitonidae are "zygodactylous perching birds with ten tail feathers" (Ripley, 1945: 542). After reviewing several previous classifications, Ripley observed the "the members of the Galbulae hardly deserve familial rank." He proposed "two families for the suborder as follows: superfamily Galbuloidea; families Galbulidae and Bucconidae; the latter to contain three subfamilies, Bucconinae, Capitoninae and Indicatorinae" (p. 543). He recognized 9 genera and 66 species of barbets. The number of species was changed to 71 in a subsequent paper (1946).

Lowe (1946) pointed out an error in Garrod's (1878c) description and figure of the palate of *Indicator* and noted "that *Indicator*, as regards its vomer, is a good way in advance of *Picus*, and other . . . Woodpeckers, on its way to become what we now think of as a Passerine vomer" (p. 106). Lowe described the palate in the woodpeckers; *Indicator* and the Picidae exhibit a "very close similarity" in this region. He also emphasized the similarities between the Pici and the Passeres and thought that the two groups should be treated as suborders of the order Passeriformes. His proposed classification assigned the families Picidae, Indicatoridae, Capitonidae and Rhamphastidae to the suborder Pici. The hoopoes were thought to be close to the Pici but, in his "final conclusion" (p. 113) Lowe did not include them in that suborder.

The mallophagan fauna of the Piciformes has affinities with that of the passerines (Clay, 1950); no Mallophaga from the Galbulidae or Bucconidae were examined.

"The presence, reduction, or absence of one toe is of no very great importance as to the relationships of birds otherwise closely allied." (Delacour, 1951b: 49.) Therefore the three-toed and four-toed woodpeckers should be placed together when other characters indicate close relationship. On this basis several genera of woodpeckers could be merged.

The jaw musculature, tongue, horny palate, ectethmoid plate, plumage and several other characters of the Piciformes were studied by Beecher (1953), who concluded that the barbets, puffbirds, toucans, woodpeckers and honeyguides are related to one another and form a natural unit. The honeyguides differ most but the differences were ascribed to specializations associated with their wax-eating and socially parasitic habits. The skulls of jacamars "suggest their close alliance with the barbets" (p. 293).

Verheyen (1955c, 1961) reviewed the characters of the Piciformes and added data from his own studies consisting primarily of skeletal measurements. He thought that the conclusions of Stresemann (1927-34) and J. Steinbacher (1937) were correct and proposed the following classification:

Order Piciformes

Suborder Galbuloidea

Family Bucconidae

Family Galbulidae

Suborder Picoidea

Family Ramphastidae

Family Capitonidae

Family Picidae (Picumninae, Picinae, Jynginae)

Family Indicatoridae

Sibley (1956) confirmed the presence of an aftershaft in the Galbulidae and of a homologous group of barbs in the Bucconidae, including *Malacoptila*. He concluded

that the *Bucconidae* should be diagnosed as possessing an aftershaft, although it is reduced in comparison with that of the *Galbulidae*.

One of the most important studies bearing upon the classification of the *Piciformes* is that of W. Bock (Bock and Miller, 1959), in which he analyzed the functional and morphological characteristics of the feet of certain groups of birds. He found that the zygodactyl foot in the truly scansorial woodpeckers can more properly be designated "ectropodactyl" because "toes two and three point forward, the fourth toe is thrust out to the . . . side at right angles . . . and the hallux usually . . . is functionless" (p. 42-43). Bock argued that the zygodactyl foot is a perching adaptation, not a climbing adaptation, and that the same is true of the anisodactyl, syndactyl and heterodactyl arrangements. These different structures represent different adaptive pathways to meet the same functional need. Bock therefore agreed with G. Steinbacher (1935) that the differences among the foot types are phylogenetic rather than functional. "The several perching- or climbing-foot types evolved because of functional demands, but the morphological differences between the types of perching feet or between those of climbing feet are the result of the different ways that birds happened to adapt to these functional demands (multiple pathways) and cannot be explained on functional grounds" (p. 41). However, Bock disagreed with Steinbacher on the taxonomic value of the foot types. He concluded (p. 42) that "although the morphological differences between the foot types serving one particular function (i.e., perching or climbing) cannot be explained on functional grounds and although the divergence between these birds may have occurred at the time the orders of birds evolved, the foot types are too rigidly tied to their function to provide reliable taxonomic characters."

Bock wrote (p. 30) that "there is little doubt that the *Pici*, the *Psittaci*, and the *Cuculidae* have all acquired their zygodactyl foot independently of one another." If this and his other conclusions are correct it also seems possible that the possession of a zygodactyl foot is an unsubstantial basis for the definition of the *Piciformes*. It seems especially appropriate to question the alliance of the *Galbulae* and the *Pici* because the two groups have little in common other than foot structure.

The paper electrophoretic patterns of the egg white proteins of seven species of woodpeckers and *Jynx torquilla* are basically alike and somewhat similar to those of passerines but no conclusions were drawn (Sibley, 1960).

Goodwin (1964) reviewed the systematics of the barbets and agreed in most respects with Ripley (1945, 1946). He did not comment upon the relationships of the barbets to other groups.

Haffer (1968) reported similarities in the pattern of molt of the wing and tail feathers between the *Galbulidae* and *Bucconidae* and supported their inclusion in the suborder *Galbuloidea*. Of the remaining piciform groups the *Capitonidae* resemble the *Galbulidae* and *Bucconidae* most closely in their molt pattern.

Cottrell (1968) reviewed the genera of puffbirds and recommended the recognition of seven genera, namely, *Bucco*, *Malacoptila*, *Micromonacha*, *Nonnula*, *Hapaloptila*, *Monasa* and *Chelidoptera* to accommodate the 32 species in the family.

Zusi and Marshall (1970) examined the pterylosis, tongue, hyoid apparatus and skull in several woodpeckers, including the rufous-bellied woodpecker (*Hypopicus hyperythrus*) of Asia. They found *Hypopicus* to be a *Dendrocopos* although it apparently feeds in part like the sapsuckers (*Sphyrapicus*) and has a tongue "hair-tufted like a brush."

From a study of the ecology and behavior of the Lewis woodpecker (*Asyndesmus lewis*) C. Bock (1970) concluded that this somewhat aberrant genus is related to *Melanerpes*, especially to the red-headed woodpecker, *Melanerpes erythrocephalus*.

Short (1970) presented evidence from plumage pattern and other aspects of

morphology that the African woodpecker genera *Campethera*, *Geocolaptes*, and *Dendropicos* are closely related to certain New World forms (e.g., *Colaptes*, *Veni-liornis*, *Piculus*).

SUMMARY

Mainly because they possess the Type 6 deep plantar tendon arrangement and have zygodactyl feet, the Piciformes have long been considered to be a natural unit. Most workers have agreed that the Capitonidae, Ramphastidae, and Picidae are closely related. The consensus is that the Indicatoridae are near allies of the barbets, which they parasitize, yet some have suggested a relationship to the cuckoos, and this possibility seems worth reinvestigating. The peripheral piciform groups are the Neotropical jacamars and puffbirds. That they are closely related to each other has seldom been questioned, but some authorities have believed that they link the Piciformes to either the Coraciiformes or the Cuculiformes. Of all non-passerine groups the Piciformes are considered to be closest to the passerines. There are numerous points in their anatomy attesting to this affinity, yet the definitive evidence to link them to one of the passerine groups is wanting.

THE EGG WHITE PROTEIN EVIDENCE

ORDER PICIFORMES

SUBORDER GALBULAE

FAMILY GALBULIDAE, Jacamars. 1/14, fig. 37.

Species examined: *Galbula ruficauda*.

FAMILY BUCCONIDAE, Puffbirds. 2/32, fig. 37.

Species examined: *Malacoptila panamensis*; *Chelidoptera tenebrosa*.

SUBORDER PICI

FAMILY CAPITONIDAE, Barbets. 2/76, fig. 37.

Species examined: *Pogoniulus bilineatus*; *Lybius torquatus*.

FAMILY INDICATORIDAE, Honeyguides. 1/12, fig. 37.

Species examined: *Indicator indicator*.

FAMILY RAMPHASTIDAE, Toucans. 0/37.

FAMILY PICIDAE, Woodpeckers. 9/210, fig. 37.

Species examined: *Jynx torquilla*; *Colaptes auratus*; *Picus viridis*; *Dryocopus martius*; *Melanerpes erythrocephalus*, *formicivorus*, *carolinus*; *Sphyrapicus varius*; *Dendropicos fuscescens*.

The egg white patterns of four of the six piciform families are surprisingly dissimilar. The patterns of the woodpeckers (including *Jynx*) are much alike. They have a rather broad, densely staining Component 18, and indistinct conalbumins which migrate anodally and cathodally to Component 18. The ovomucoid and ovalbumin, migrating about 5 cm and 6.5 cm respectively, are each a single band. Even in fresh material they are not well defined, and they do not appear to be subdivided.

The patterns of the barbets *Lybius* and *Pogoniulus* are similar to each other and agree with those of the woodpeckers in all aspects of Component 18, the conalbumins, and the ovomucoid. The only major difference is that the ovalbumin migrates more slowly than that of woodpeckers.

The patterns of the puffbirds *Chelidoptera* and the jacamar *Galbula* show many similarities. They differ from the pattern of the woodpeckers in all aspects. The conalbumins appear as three or four dense bands and migrate just off the origin toward the anode, masking Component 18. At about 4 cm from the origin there are some small, but well-defined bands, and anodal to these is a rather broad, indistinct band. A distinct ovomucoid thus is not apparent. There is a single, sharp ovalbumin, which migrates ahead of that of the woodpeckers. In all the features in which the patterns of the jacamar and puffbird differ from those of the Pici they agree with those of the kingfishers.

The patterns of the woodpeckers and barbets do not closely resemble those of any other non-passerine group. They show a general similarity to the patterns of the Trochilidae and Caprimulgidae but differ from these in a number of details. The woodpecker pattern is somewhat like the Type B passerine pattern (*sensu* Sibley, 1970), but the likeness is not great enough to form the basis for a decision.

The pattern of *Galbula* differs from the pattern of the woodpeckers in many aspects. The conalbumins appear as three or four dense bands and migrate just off the origin toward the anode, masking Component 18. At about 4 cm from the origin there are some small, but well-defined bands, and anodal to these is a rather broad, indistinct band. A distinct ovomucoid thus is not apparent. There is a single, sharp ovalbumin, which migrates ahead of that of the woodpeckers. In those features in which the pattern of *Galbula* differs from those of the Pici it agrees with those of the kingfishers. The pattern of the puffbird *Chelidoptera* is similar to that of *Galbula*.

The pattern of *Indicator* differs from those of the other Piciformes. The ovomucoid and ovalbumin migrates faster than those of the woodpeckers, and the conalbumins are more strongly defined. There are a number of similarities between the pattern of *Indicator* and those of the cuckoo *Cuculus* and the coucal *Centropus*.

The patterns of the woodpeckers and barbets do not closely resemble those of any other non-passerine group. They show a general similarity to the patterns of the Trochilidae and Caprimulgidae but differ from these in a number of details. The woodpecker pattern is somewhat like the Type B passerine pattern (*sensu* Sibley, 1970), but the likeness is not great enough to form the basis for a decision.

CONCLUSIONS

The barbets and woodpeckers seem to be closely allied. Their nearest relatives may lie among the passerines or with some non-passerine group. Our evidence does not support a close relationship between the honeyguides and the barbets. We suggest that the question of the relationships of the Indicatoridae be reopened with critical comparisons to the Cuculidae. The Galbulidae, and perhaps the Bucconidae, also may not be piciform. They may be most closely allied to the Alcedinidae. We urge study of this suggestion at all levels in order to determine the precise nature of the relationships involved.

PROBABILITIES AND POSSIBILITIES

Sibley (1970: 114–117) summarized the status of certain passerine systematic problems with a series of statements under the headings “Highly Probable,” “Probable,” “Possible,” and “Improbable.” This has proved to be an effective method for expressing the different degrees of confidence we attach to our “conclusions.” We therefore present below a similar series of statements which serve as synopses of the principal conclusions of the present paper. These statements refer both to previously proposed alliances and to suggestions put forth in this paper. They reflect our interpretation of the electrophoretic data and our evaluation of the evidence from other sources.

HIGHLY PROBABLE

Our understanding of a few problems is now advanced enough so that we can consider them to be solved.

It is highly probable that—

- 1) the large ratites (*Struthio*, *Rhea*, *Dromaius*, *Casuarius*) are monophyletic and evolved from a flying ancestor;
- 2) *Pelecanoides* is a member of the Procellariiformes and is only convergently similar to the Alcidae;
- 3) *Cochlearius* is most closely allied to the Ardeidae, particularly to the night herons (*Nycticorax*);
- 4) the flamingos are more closely related to the Ciconiiformes than to the Anseriformes, although all three groups had a common ancestor;
- 5) *Opisthocomus* is a cuckoo, closely allied to the Neotropical Crotophaginae;
- 6) the Alcidae are closely related to the other charadriiform birds;
- 7) *Tyto* is closely related to the strigid owls;
- 8) the woodpeckers and barbets are closely allied.

PROBABLE

For other problem taxa reasonable certainty exists regarding their relationships. Conclusive proof of these alliances, however, remains to be presented and in many cases additional details need to be worked out.

It is probable that—

- 1) the nearest relatives of the penguins are the Procellariiformes;
- 2) the tinamous are most closely allied to the Galliformes;

- 3) a close relationship exists among *Sula*, *Pelecanus*, *Phalacrocorax*, and *Anhinga*;
- 4) *Scopus* belongs to the Ciconiidae;
- 5) the New World vultures are closer to the other diurnal raptors than to the storks;
- 6) within the Gruiformes a natural assemblage consisting of the Gruidae, Aramidae, Rallidae, Eurypyidae, Heliornithidae, and Turnicidae can be recognized;
- 7) among caprimulgiforms two natural groups exist, one consisting of the Aegothelidae and Podargidae, the other including the Caprimulgidae, Nyctibiidae, and Steatornithidae;
- 8) the swifts and hummingbirds are more closely related to each other than either is to any other group;
- 9) the Coraciiformes of Wetmore are polyphyletic;
- 10) the closest allies of the todies are the kingfishers.

POSSIBLE

A 50 percent level of probability is represented by the following statements, hence they could also be rephrased as questions. They are among the most interesting and controversial problems of non-passerine systematics.

It is possible that—

- 1) a distant relationship exists between *Apteryx* and a tinamou-galliform assemblage;
- 2) the loons are more closely related to the Charadriiformes than to any other living group;
- 3) the Phaethontidae and Fregatidae are not closely allied to the other Pelecaniformes;
- 4) the nearest relatives of the Pelecaniformes are the Ciconiiformes;
- 5) the diurnal birds of prey may be allied to the owls through the Falconidae;
- 6) the nearest relatives of the Jacanidae are the Rostratulidae;
- 7) *Pterocles* is more closely allied to the shorebirds than to the pigeons;
- 8) the closest allies of the parrots are the pigeons;
- 9) the colies are related to the swifts;
- 10) the Galbulidae are more closely related to the Alcedinidae than to the Picidae.

IMPROBABLE

A number of opinions, formerly widely believed, have been discredited.

It is improbable that—

- 1) a close relationship exists between *Rhea* and the tinamous;
- 2) the loons are most nearly allied to the grebes;
- 3) *Pandion* deserves familial status in the Falconiformes;
- 4) *Opisthocomus* is galliform;
- 5) swifts are closely related to the Caprimulgiformes;
- 6) the closest relatives of *Indicator* are the barbets.

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In previous papers (Sibley, 1960, 1970) a list of all persons who had contributed egg white specimens up to that time was included. We are following this precedent in the present list because it seems unlikely that further monographic surveys will be published. Future papers will probably relate to more restricted problems and the acknowledgments will include only those who collected the specimens for a given problem.

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EPILOGUE

This study is not completed with the publication of this paper. Indeed, it is but barely begun. The starch-gel technique is not capable of resolving many or even most of the proteins in avian egg white and thus it has not been able to provide us with data of sufficient precision to solve most problems. We therefore regard this paper as a stage in the development of "molecular systematics," not as a definitive statement.

Its main contribution is seen by its authors as a review of the literature and a definition of the major problems. Most answers still lie ahead.

But the future is remarkably bright. While this manuscript was being written we began to work with an impressive new technique called "isoelectric focusing in acrylamide gel," or IFAG, which characterizes proteins by their isoelectric point properties. The resolving power of IFAG is several times greater than that of starch gel and we now know that avian egg white contains at least 20 to 30 proteins in most species and over 30 in some. The resulting patterns are so informative that significant comparisons at the level of genera and species are now routinely possible. A paper on the ratites has been completed (Sibley and Frelin, in press) and will be published in *The Ibis*, in 1972. It will mark the beginning of a series of studies of problems, many of which have been reviewed and defined in the present study or in that by Sibley (1970) on the passerines.

It is also clear that other protein systems, notably the red blood cell proteins, are potential sources of taxonomic information. And techniques will continue to improve so that the vast, unexplored store of taxonomic information sequestered in avian proteins can and will be exploited. Amino acid sequencing, peptide comparisons and other techniques have as yet hardly been utilized. Let no one assume that any problem of systematic relationships is hopeless until it has at least been examined with one or more of these techniques.

As is apparent from the long list of names in the Acknowledgments section this type of research requires the interest and help of many persons. The need for this help will continue and we urge that those with the requisite knowledge and interest to save egg white or blood proteins do so whenever possible. Such material is taking its place in collections along with traditional specimen material and we predict that biochemical equipment will be as indispensable to the next generation of systematists as the calipers and scalpel have been in the past.

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FIGURES 2 to 37

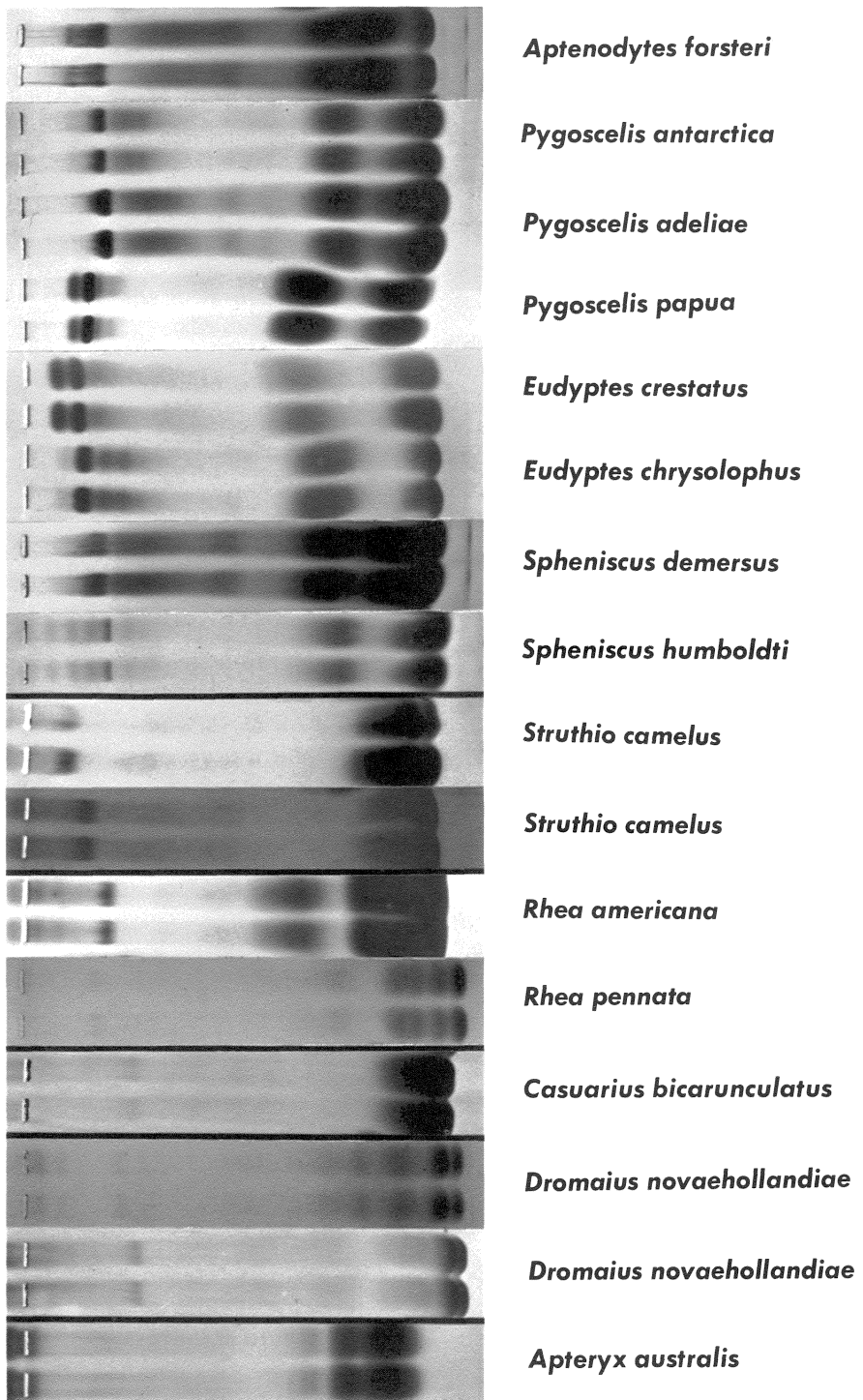


FIG. 2. Starch gel electrophoretic patterns of the Spheniscidae, Struthionidae, Rheidae, Casuariidae, Dromaiidae, and Apterygidae (part).

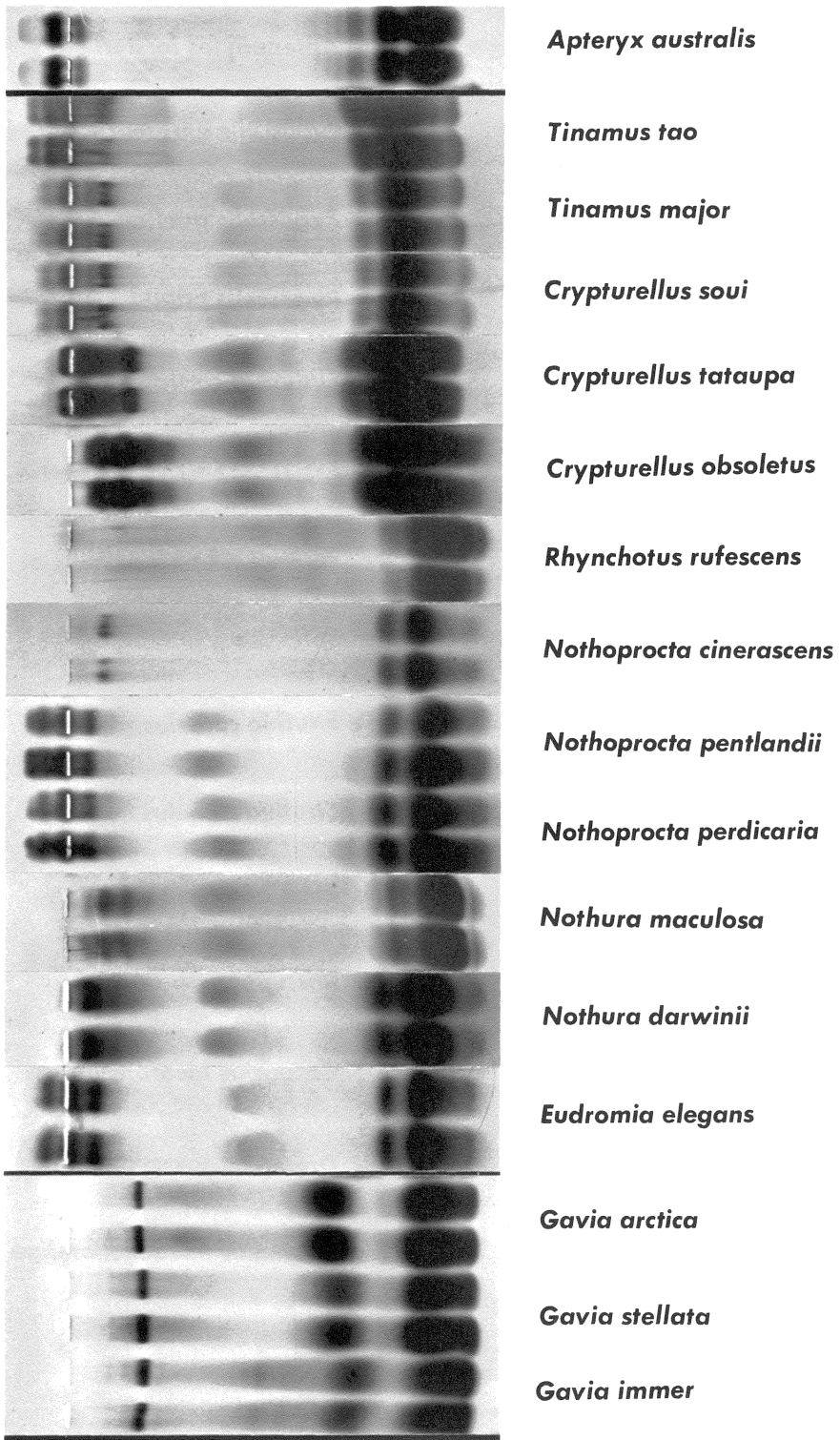


FIG. 3. Starch gel electrophoretic patterns of the Apterygidae (part), Tinamidae, and Gaviidae.

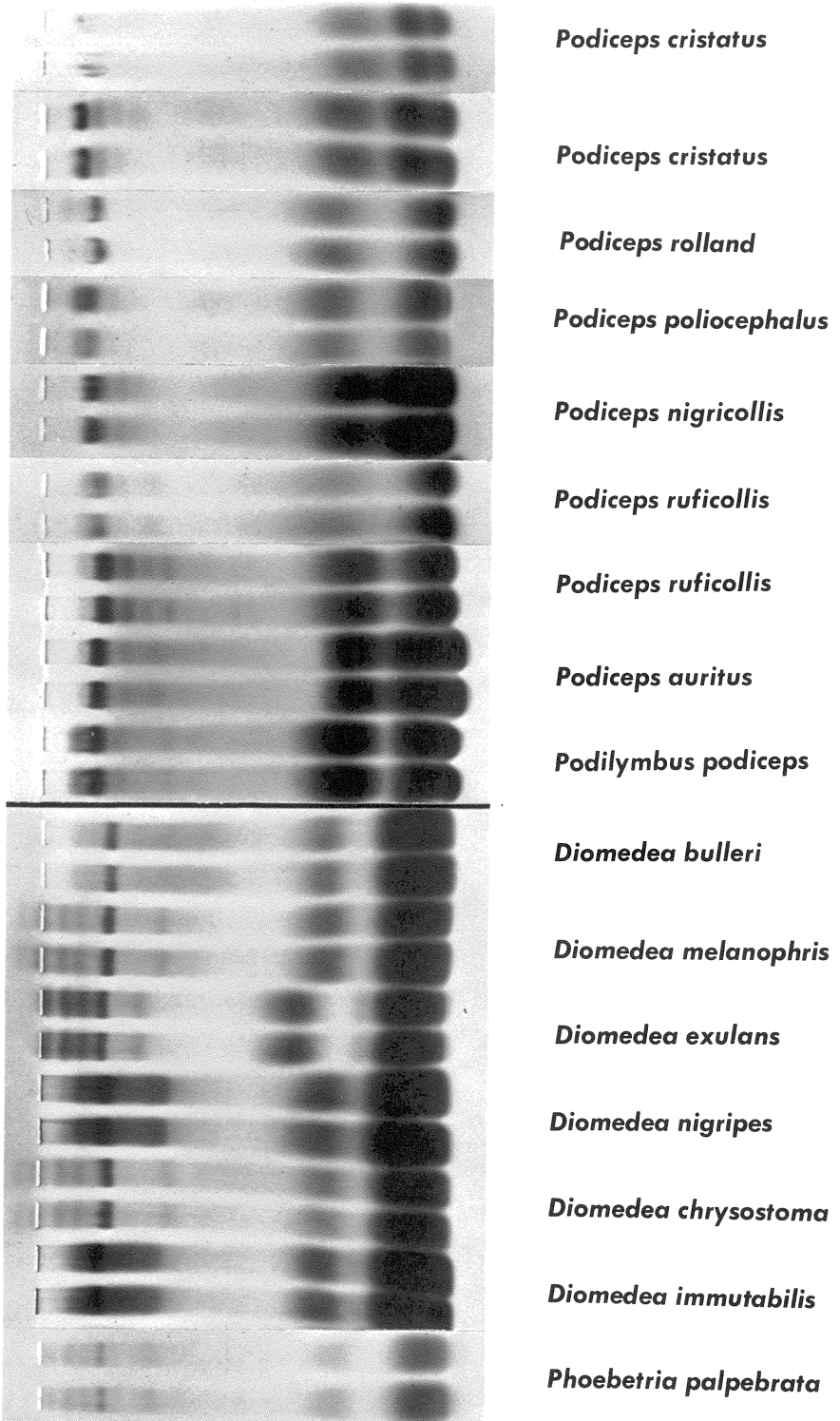


FIG. 4. Starch gel electrophoretic patterns of the Podicipedidae and Diomededidae.

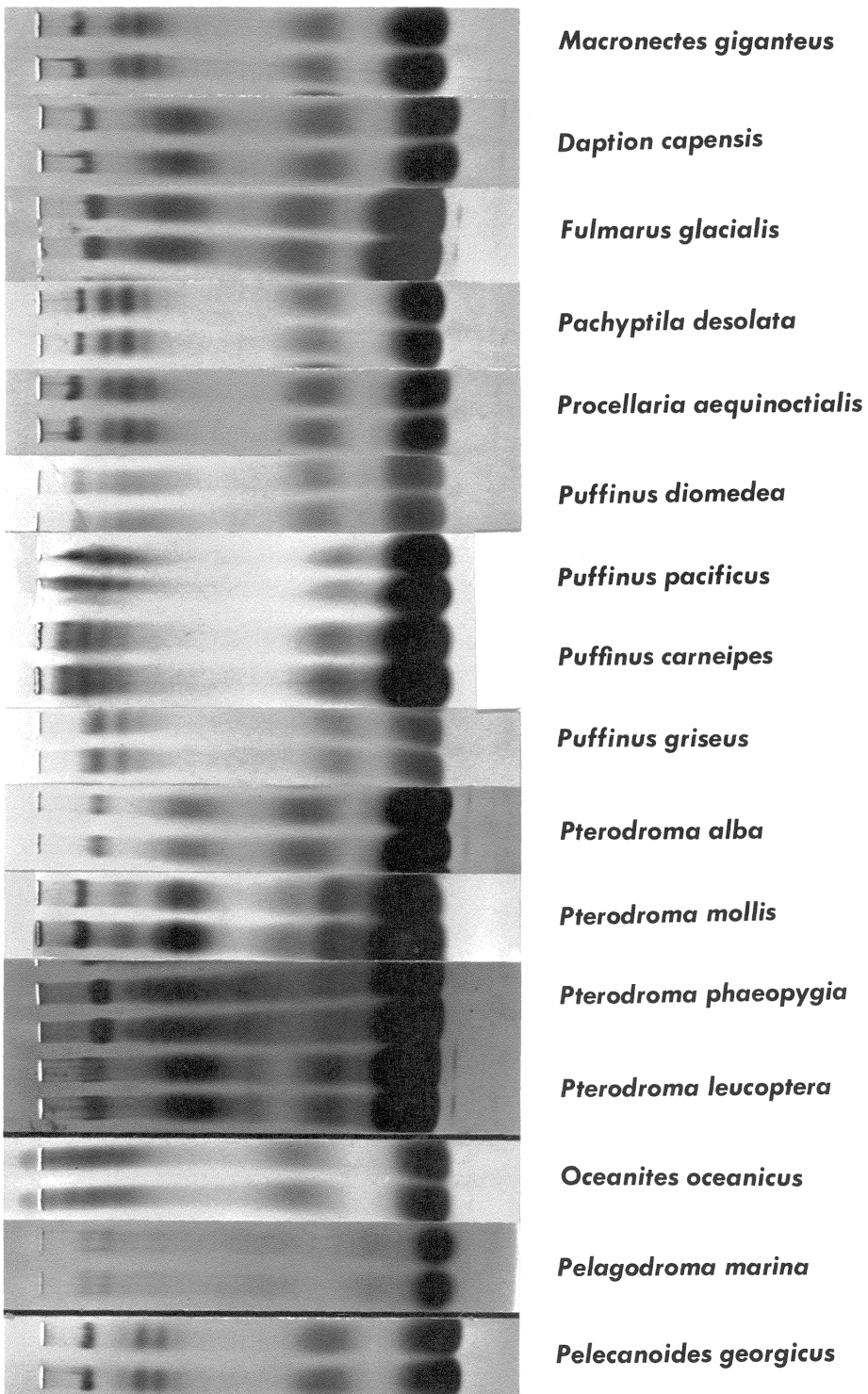


FIG. 5. Starch gel electrophoretic patterns of the Procellariidae, Hydrobatidae, and Pelecanoididae (part).

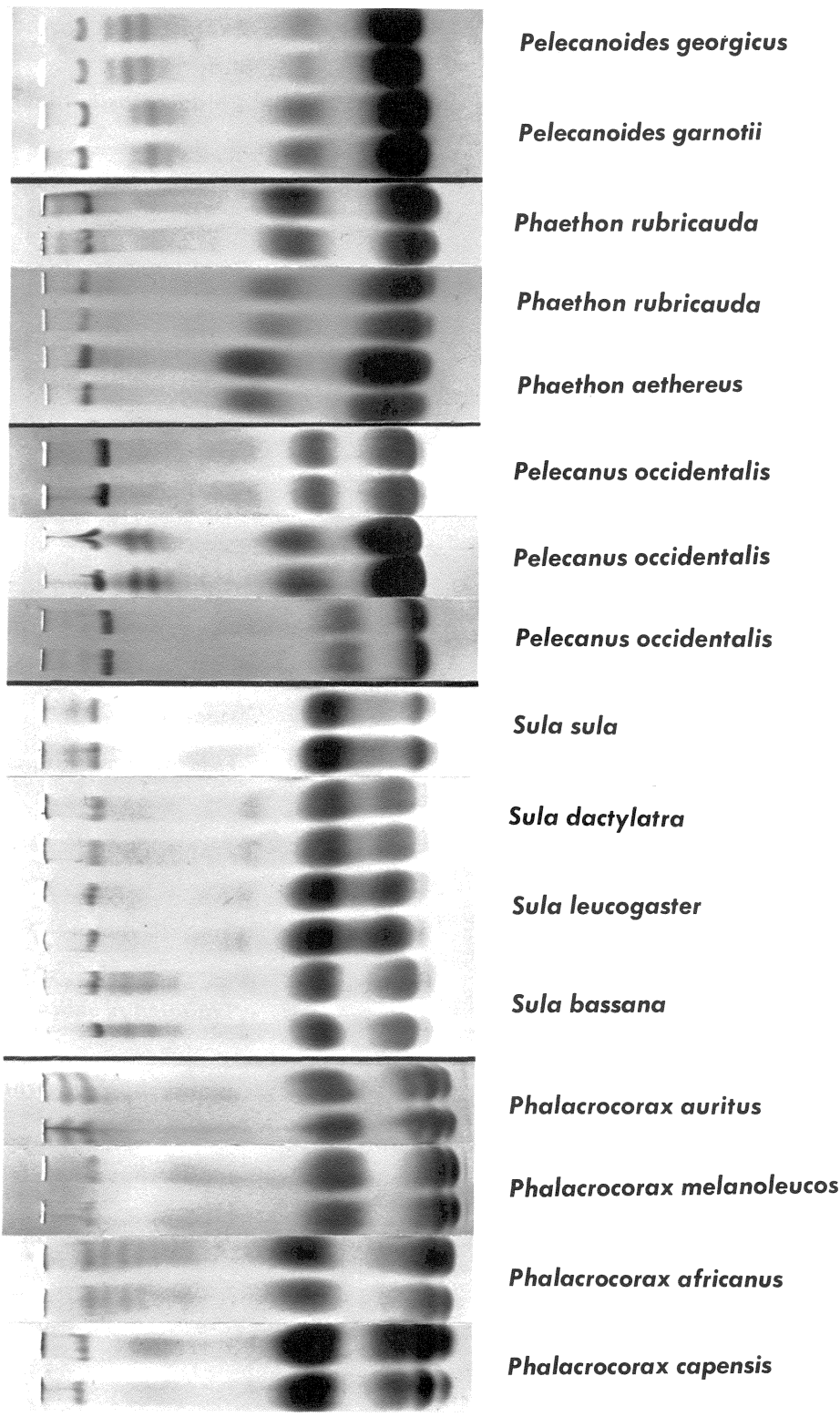


FIG. 6. Starch gel electrophoretic patterns of the Pelecanooididae (part), Phaethonidae, Pelecanidae, Sulidae, and Phalacrocoracidae (part).

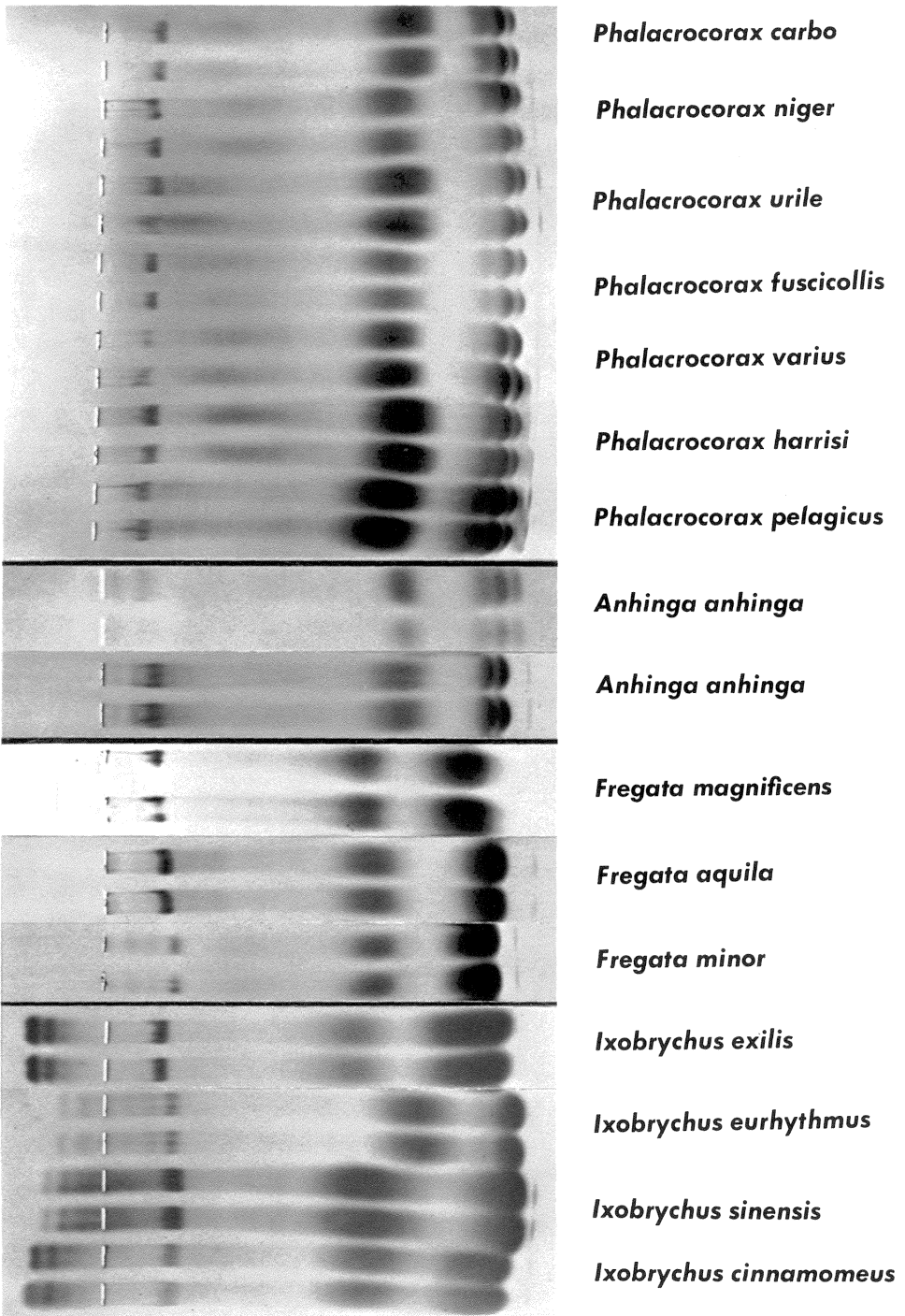


FIG. 7. Starch gel electrophoretic patterns of the Phalacrocoracidae (part), Anhimidae, Fregatidae, and Ardeidae (part).

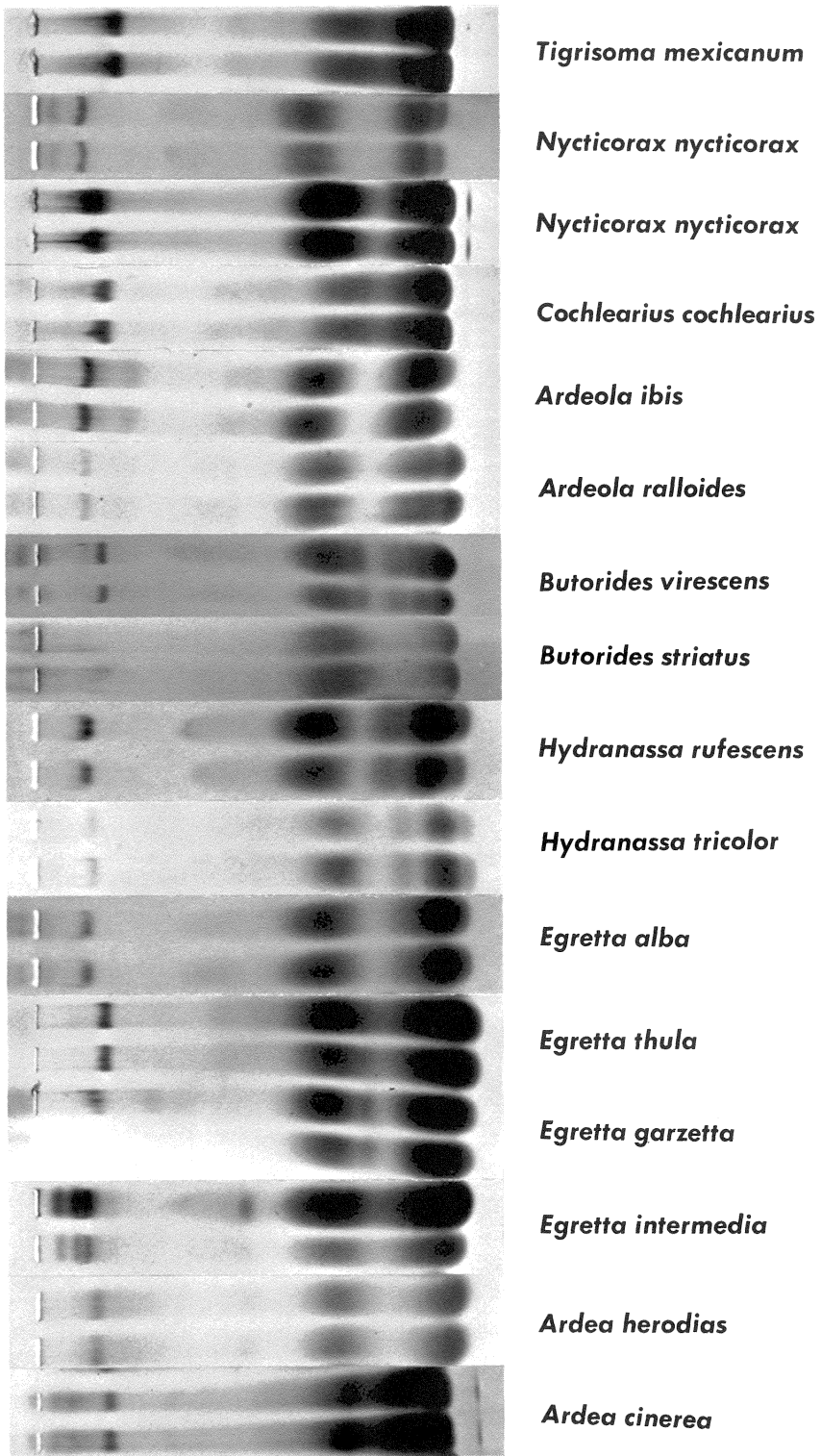
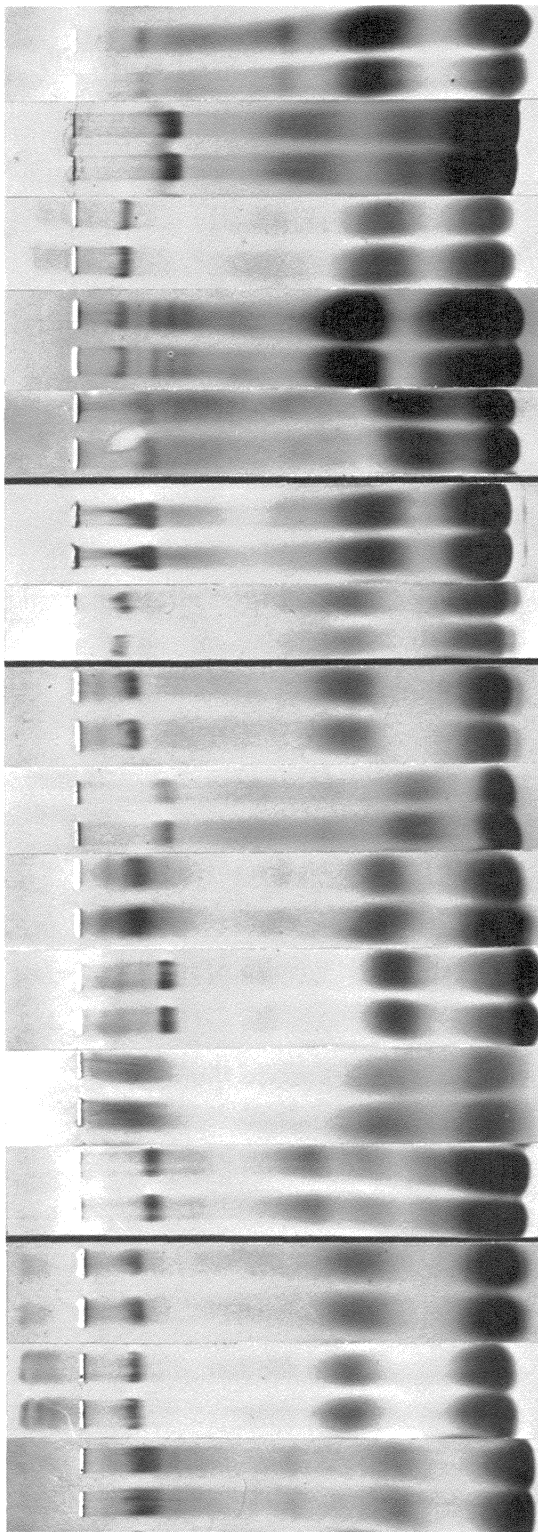


FIG. 8. Starch gel electrophoretic patterns of the Ardeidae (part).



Ardea cocoi

Ardea sumatrana

Ardea melanocephala

Ardea novaehollandiae

Agamia agami

Scopus umbretta

Scopus umbretta

Mycteria americana

Ibis leucocephalus

Anastomus oscitans

Ciconia ciconia

Ciconia nigra

Leptoptilos javanicus

Threskiornis spinicollis

Threskiornis aethiopica

Threskiornis melanocephala

FIG. 9. Starch gel electrophoretic patterns of the Ardeidae (part), Scopidae, Ciconiidae, and Threskiornithidae (part).

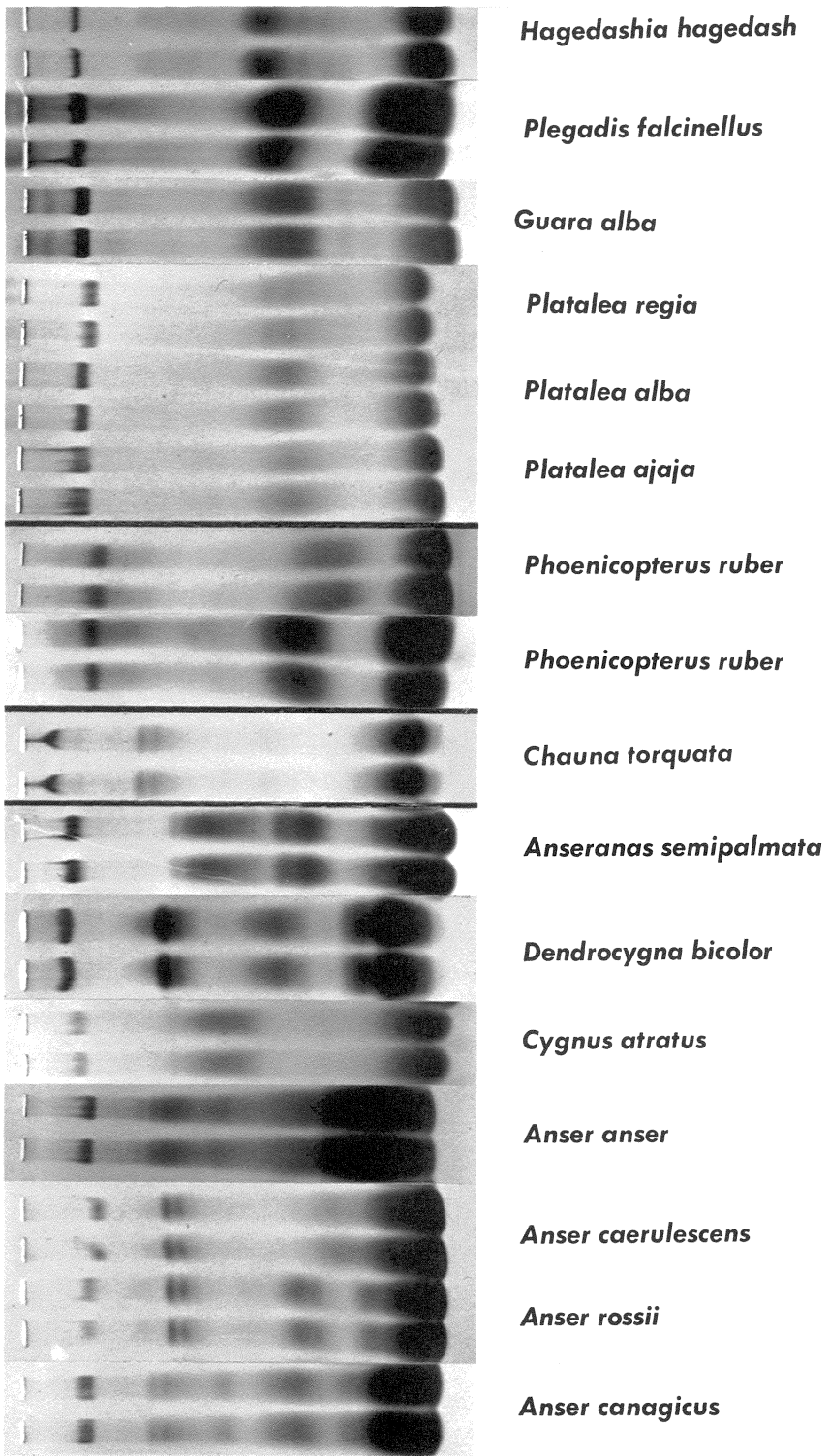


FIG. 10. Starch gel electrophoretic patterns of the Threskiornithidae (part), Phoenicopteridae, Anhimidae, and Anatidae (part).

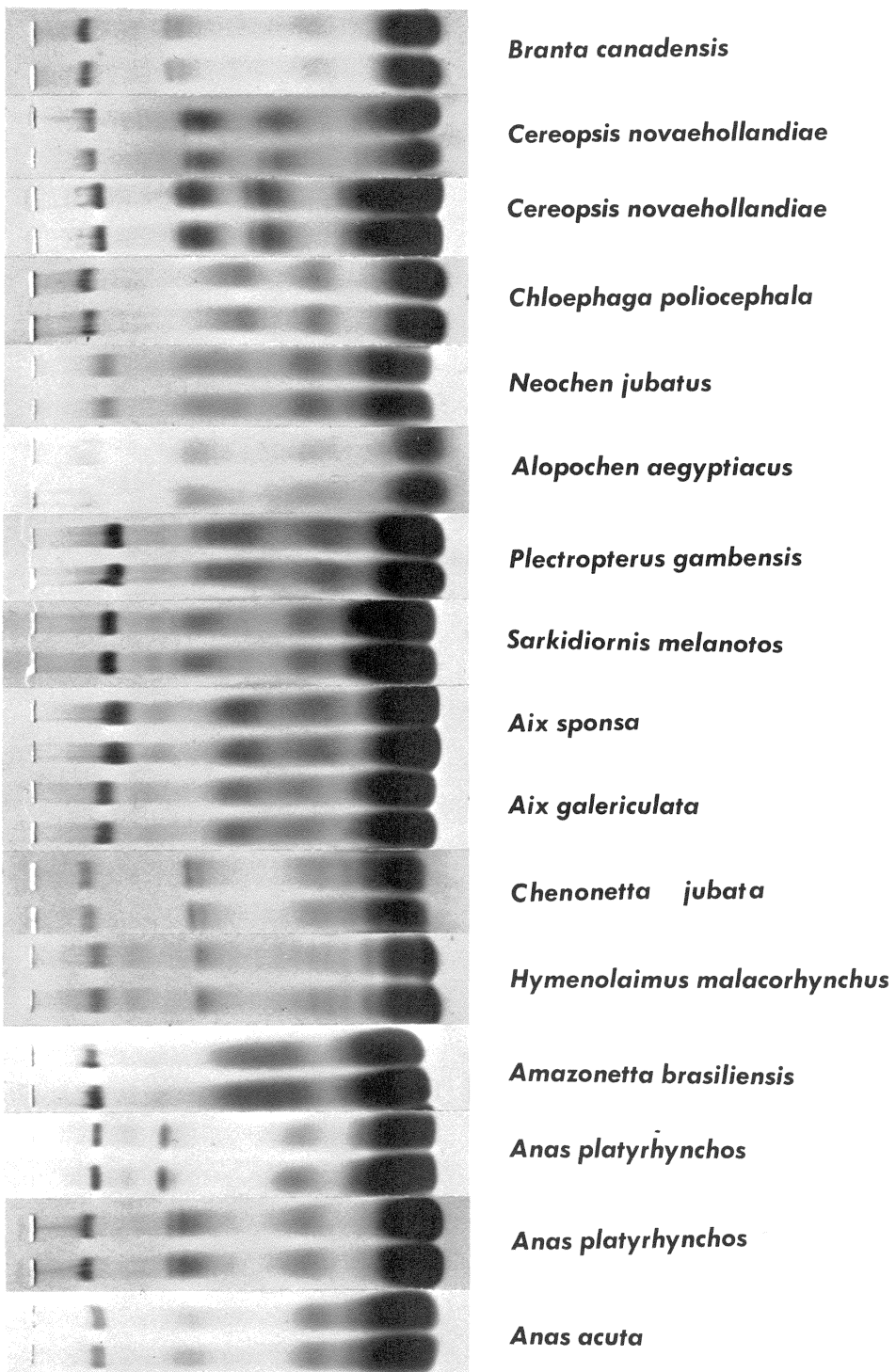


FIG. 11. Starch gel electrophoretic patterns of the Anatidae (part).

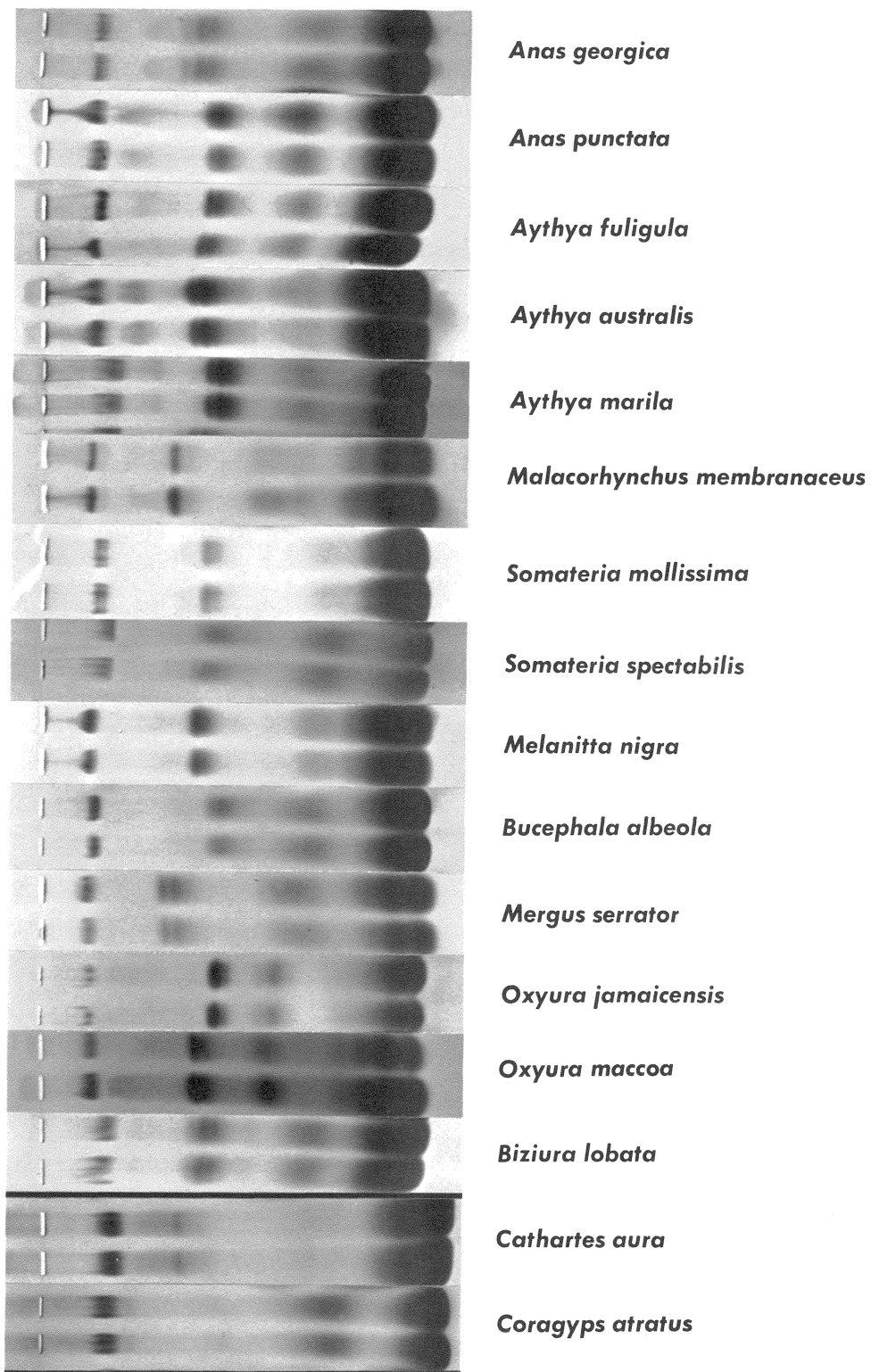
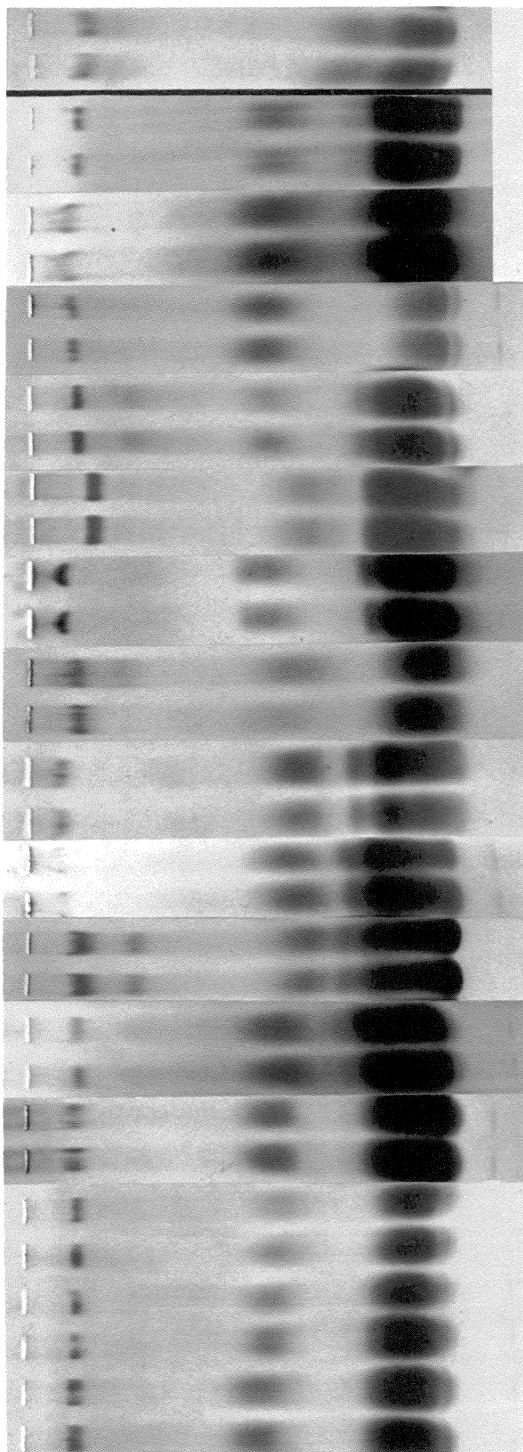


FIG. 12. Starch gel electrophoretic patterns of the Anatidae (part) and Cathartidae.



Pandion haliaetus

Pernis apivorus

Machaerhamphus alcinus

Elanus leucurus

Elanus caeruleus

Ictinia mississippiensis

Milvus migrans

Haliaeetus sphenurus

Gyps africanus

Gyps coprotheres

Torgos tracheliotus

Circaetus gallicus

Spilornis cheela

Circus pygargus

Circus aeruginosus

Circus cyaneus

FIG. 13. Starch gel electrophoretic patterns of the Pandionidae and Accipitridae (part).

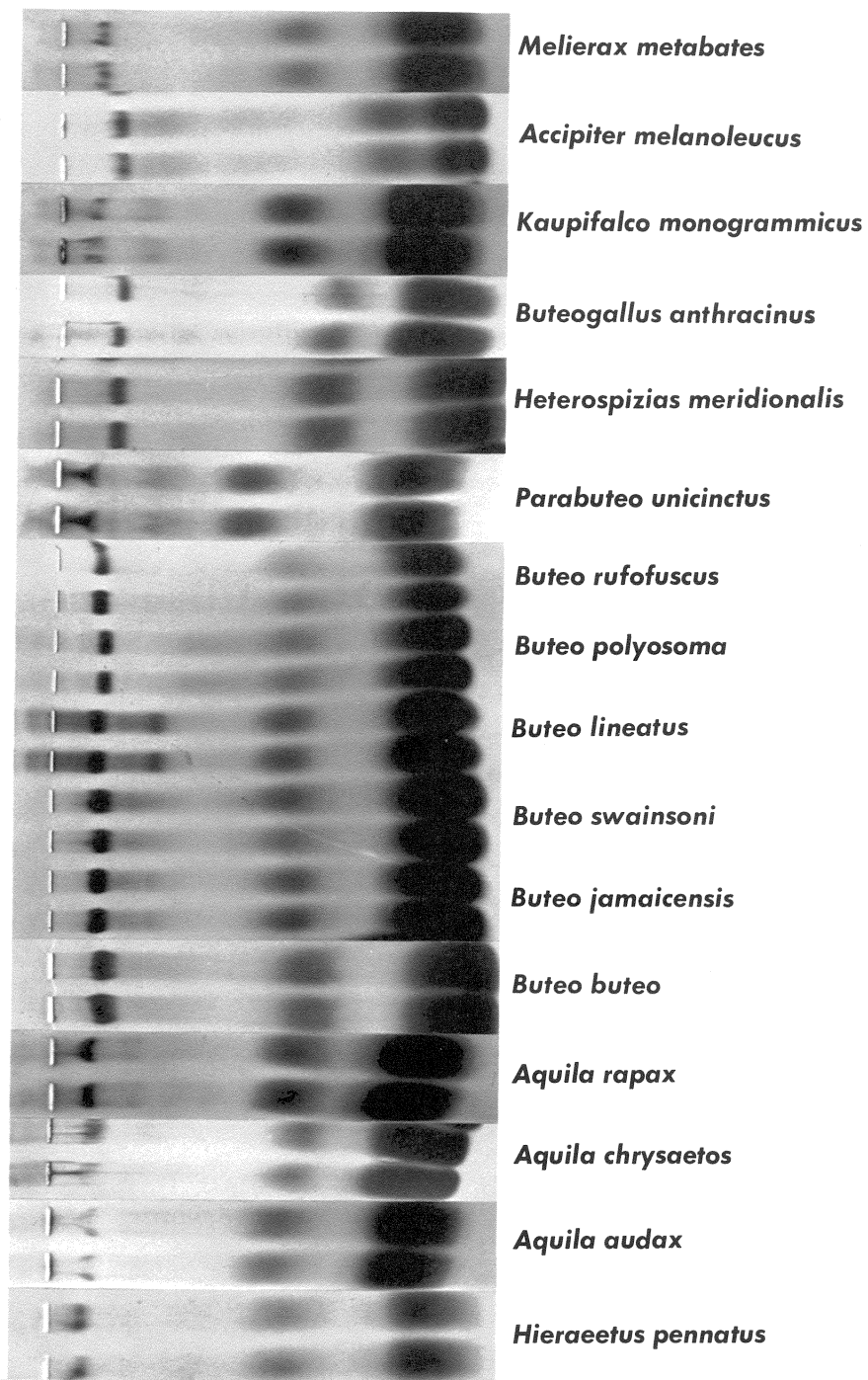


FIG. 14. Starch gel electrophoretic patterns of the Accipitridae (part).

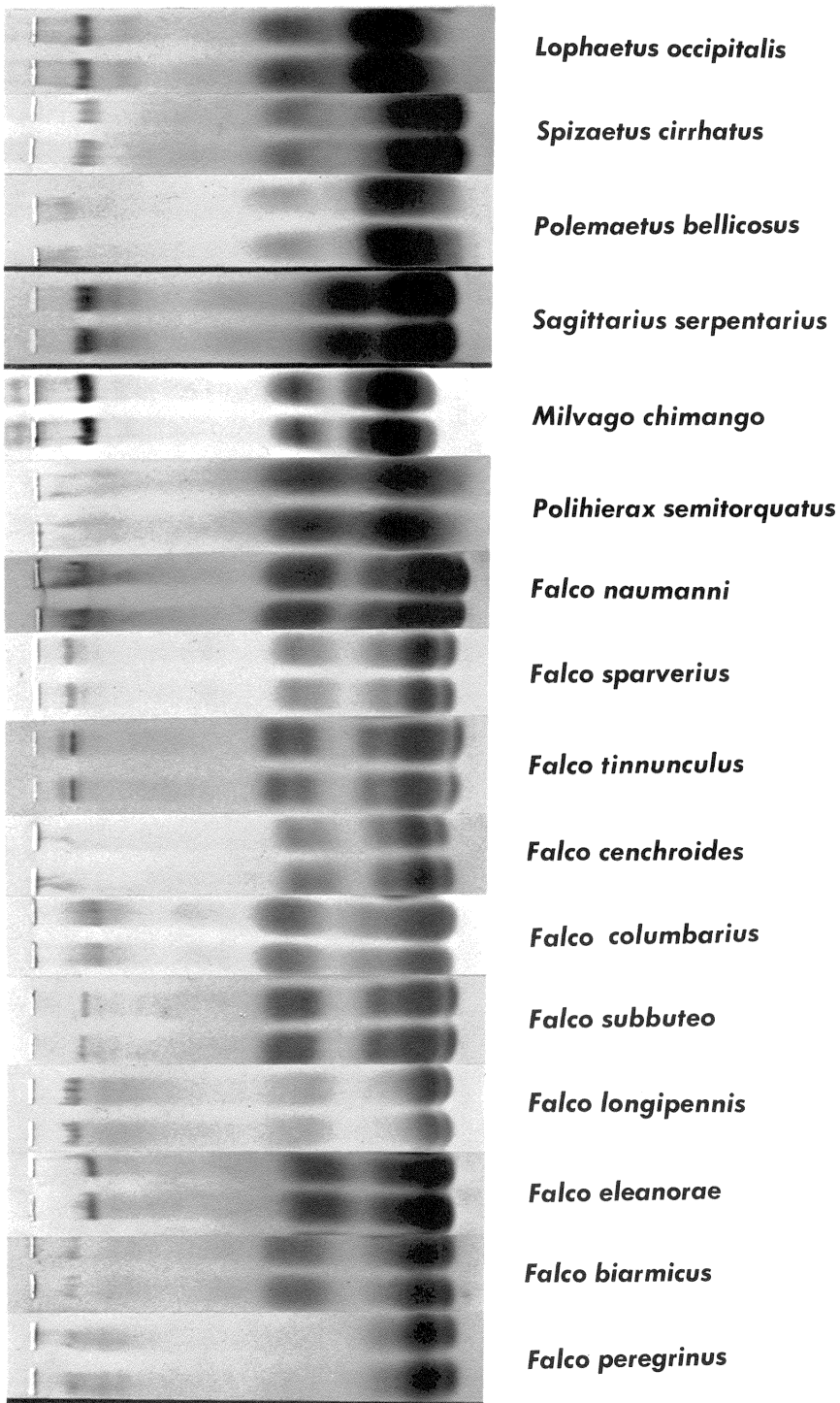


FIG. 15. Starch gel electrophoretic patterns of the Accipitridae (part), Sagittariidae, and Falconidae.

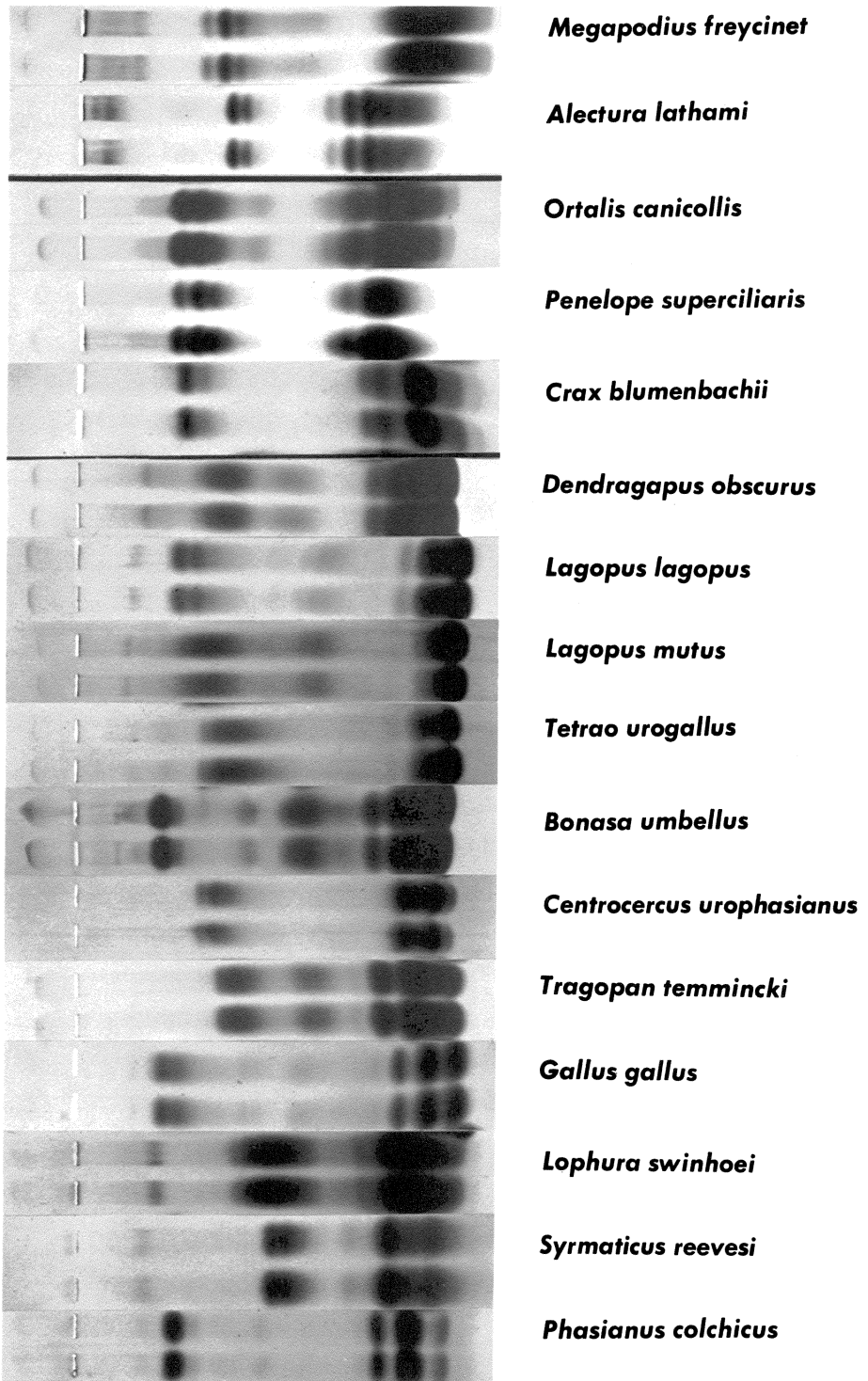


FIG. 16. Starch gel electrophoretic patterns of the Megapodiidae, Cracidae, and Phasianidae (part).

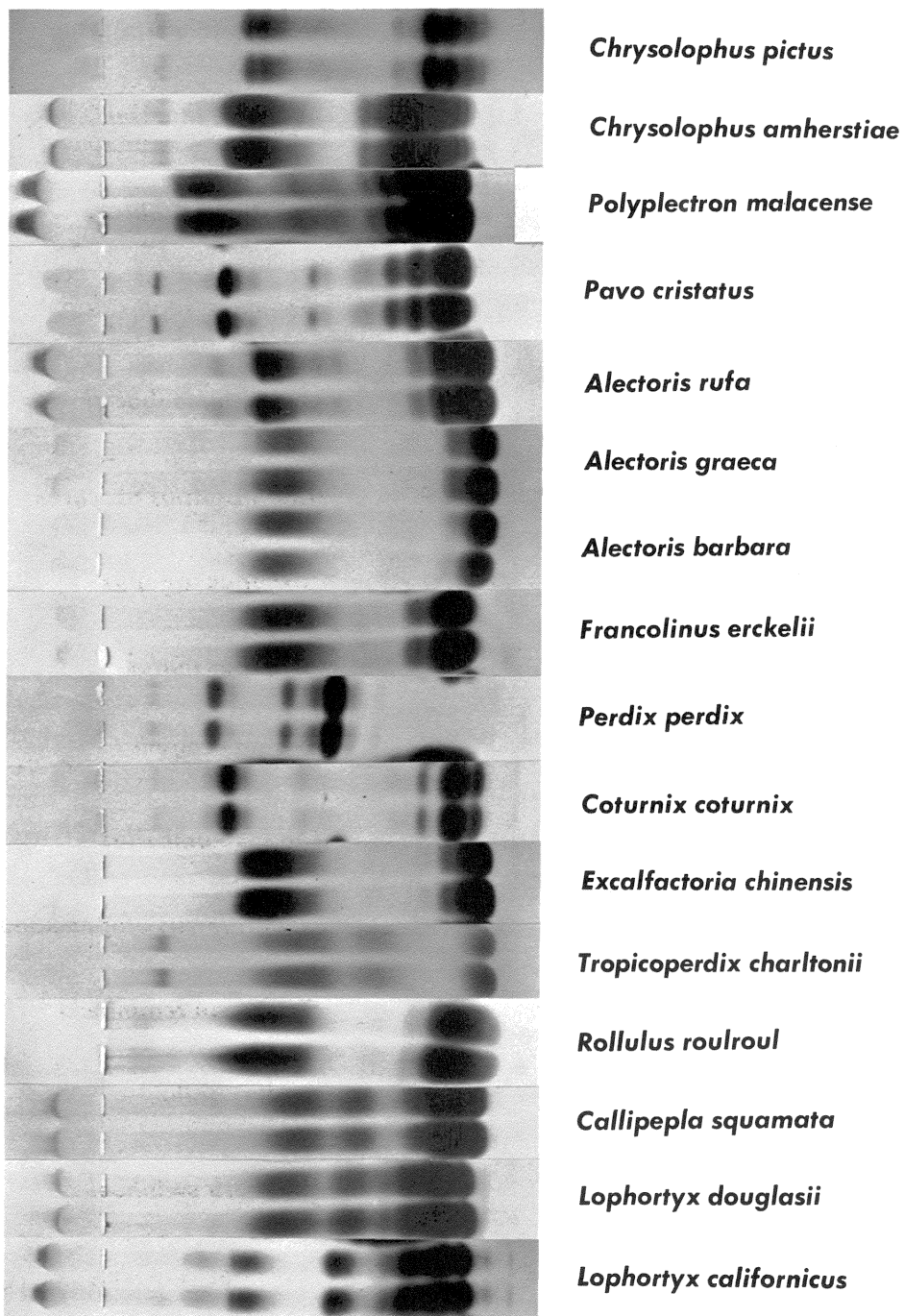


FIG. 17. Starch gel electrophoretic patterns of the Phasianidae (part).

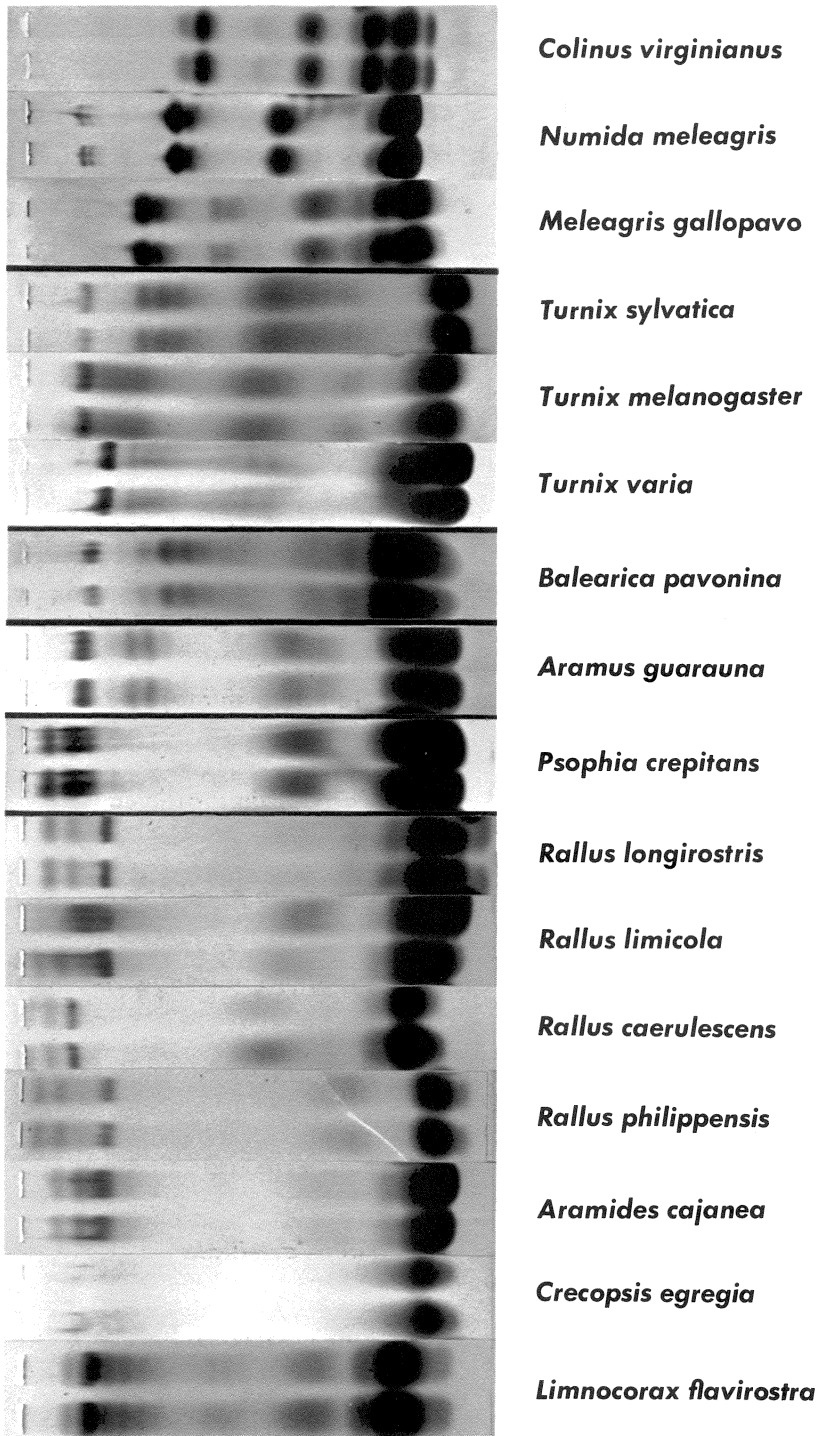


FIG. 18. Starch gel electrophoretic patterns of the Phasianidae (part), Turnicidae, Gruidae, Aramidae, Psophiidae, and Rallidae (part).

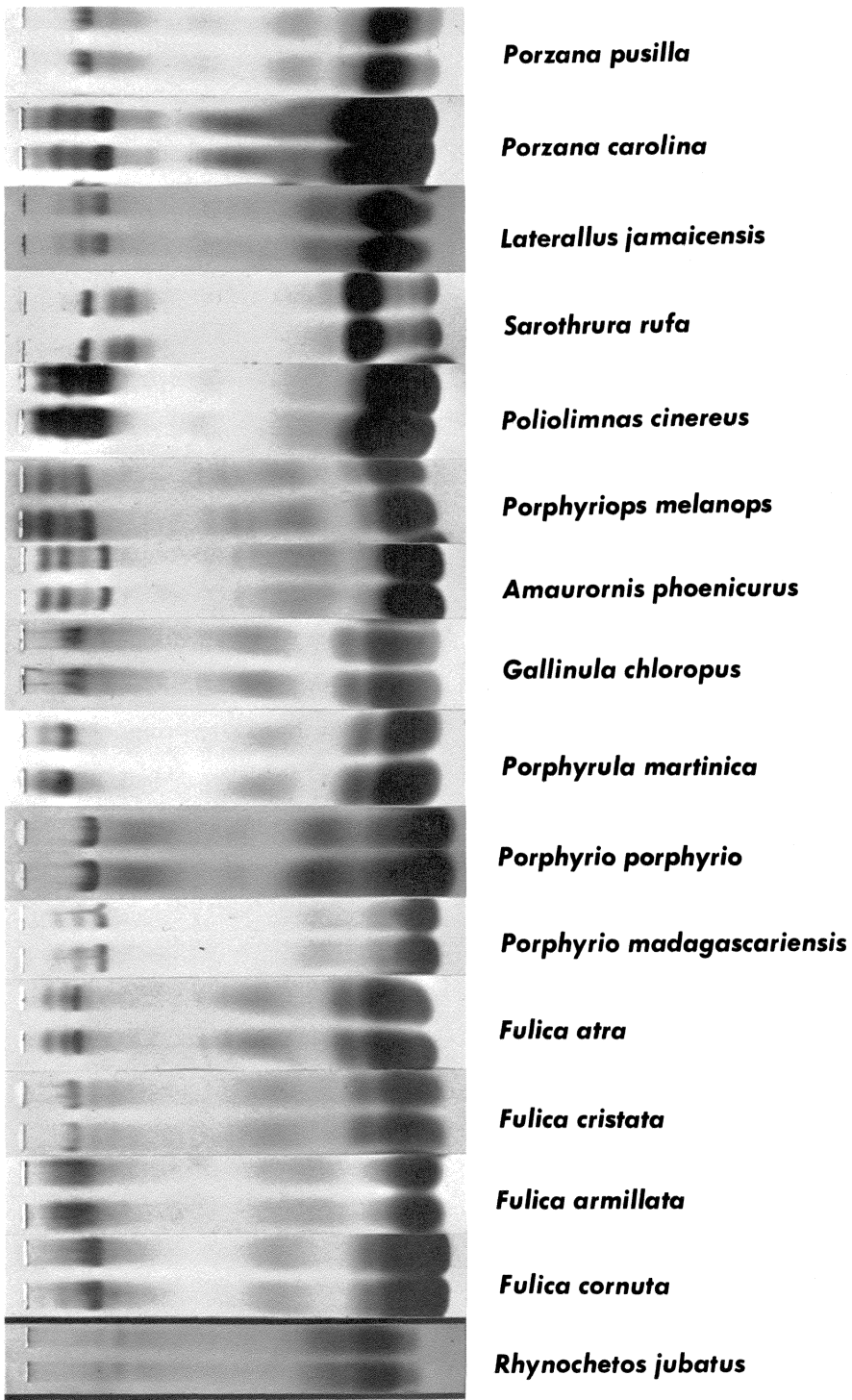


FIG. 19. Starch gel electrophoretic patterns of the Rallidae (part) and Rhynochetidae.

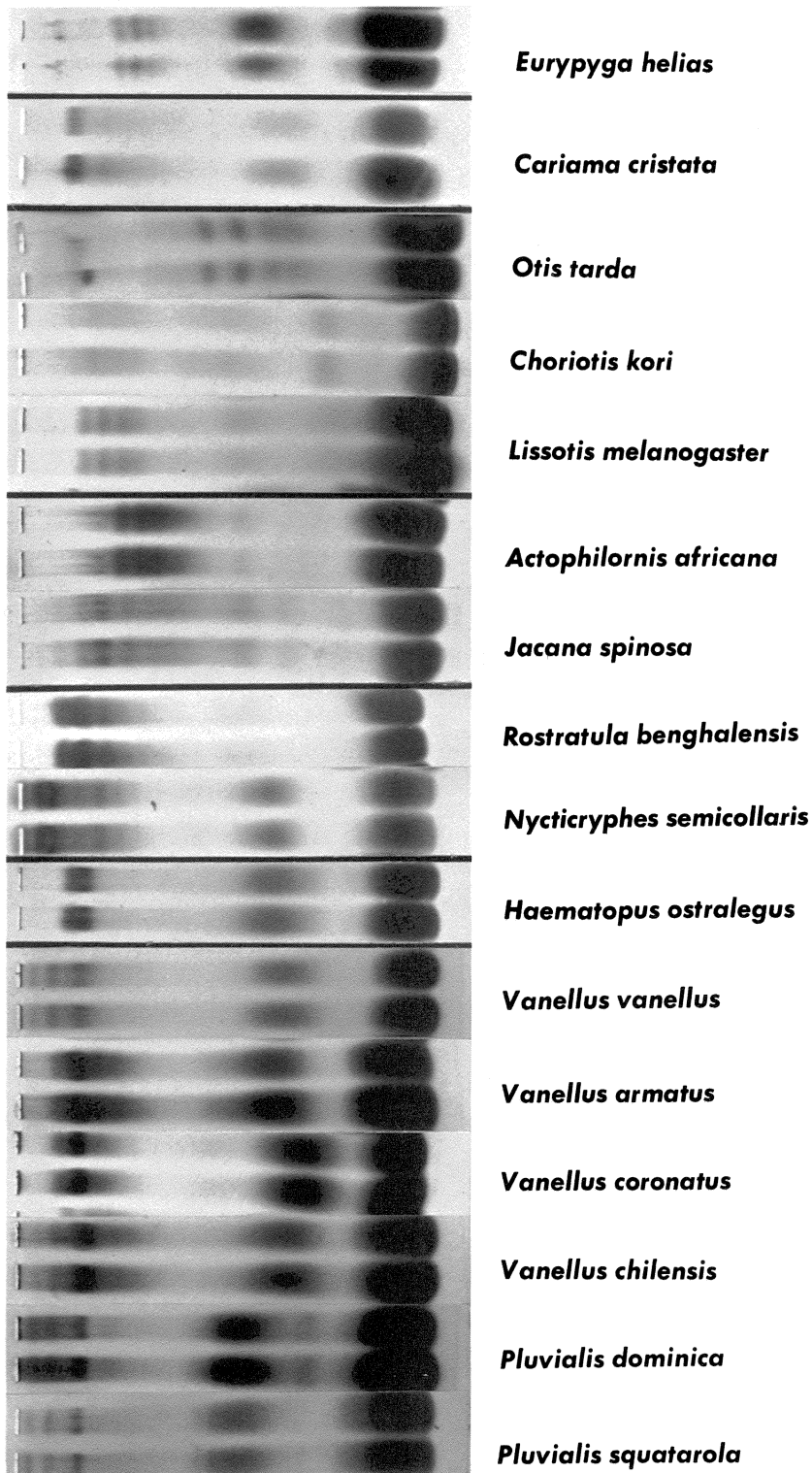
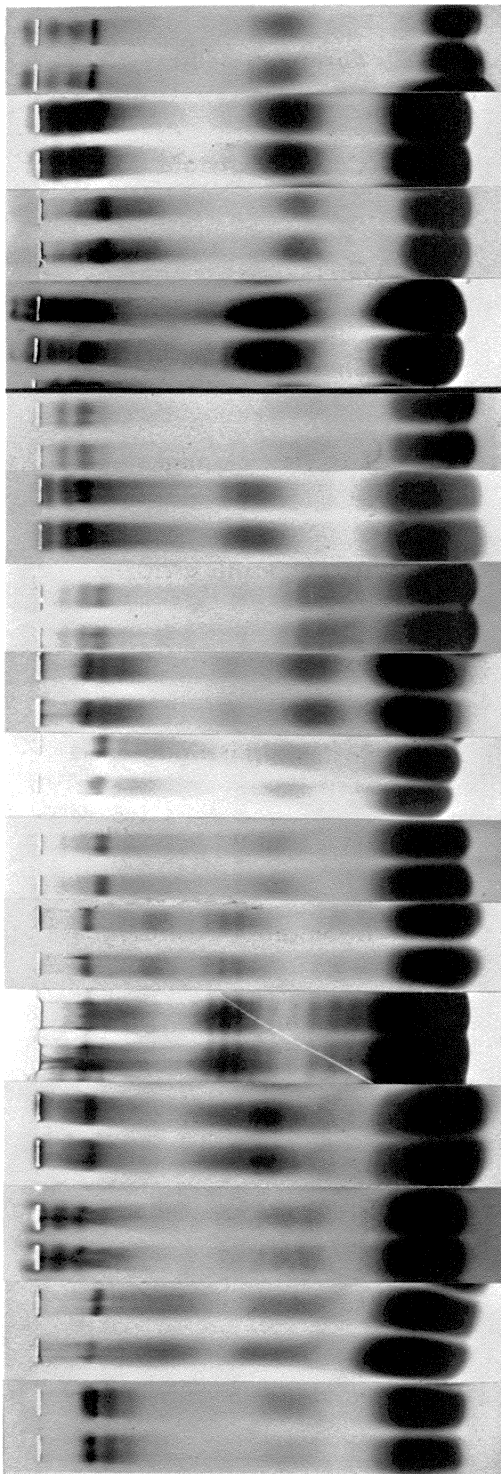


FIG. 20. Starch gel electrophoretic patterns of the Eurypygidae, Cariamidae, Otididae, Jacanidae, Rostratulidae, Haematopodidae, and Charadriidae (part).



Charadrius hiaticula

Charadrius dubius

Charadrius melanops

Eudromias morinellus

Limosa limosa

Limosa haemastica

Numenius phaeopus

Tringa totanus

Catoptrophorus semipalmatus

Arenaria interpres

Gallinago gallinago

Gallinago gallinago

Gallinago paraguaiiae

Calidris canutus

Calidris pusilla

Calidris maritima

FIG. 21. Starch gel electrophoretic patterns of the Charadriidae (part) and Scolopacidae (part).

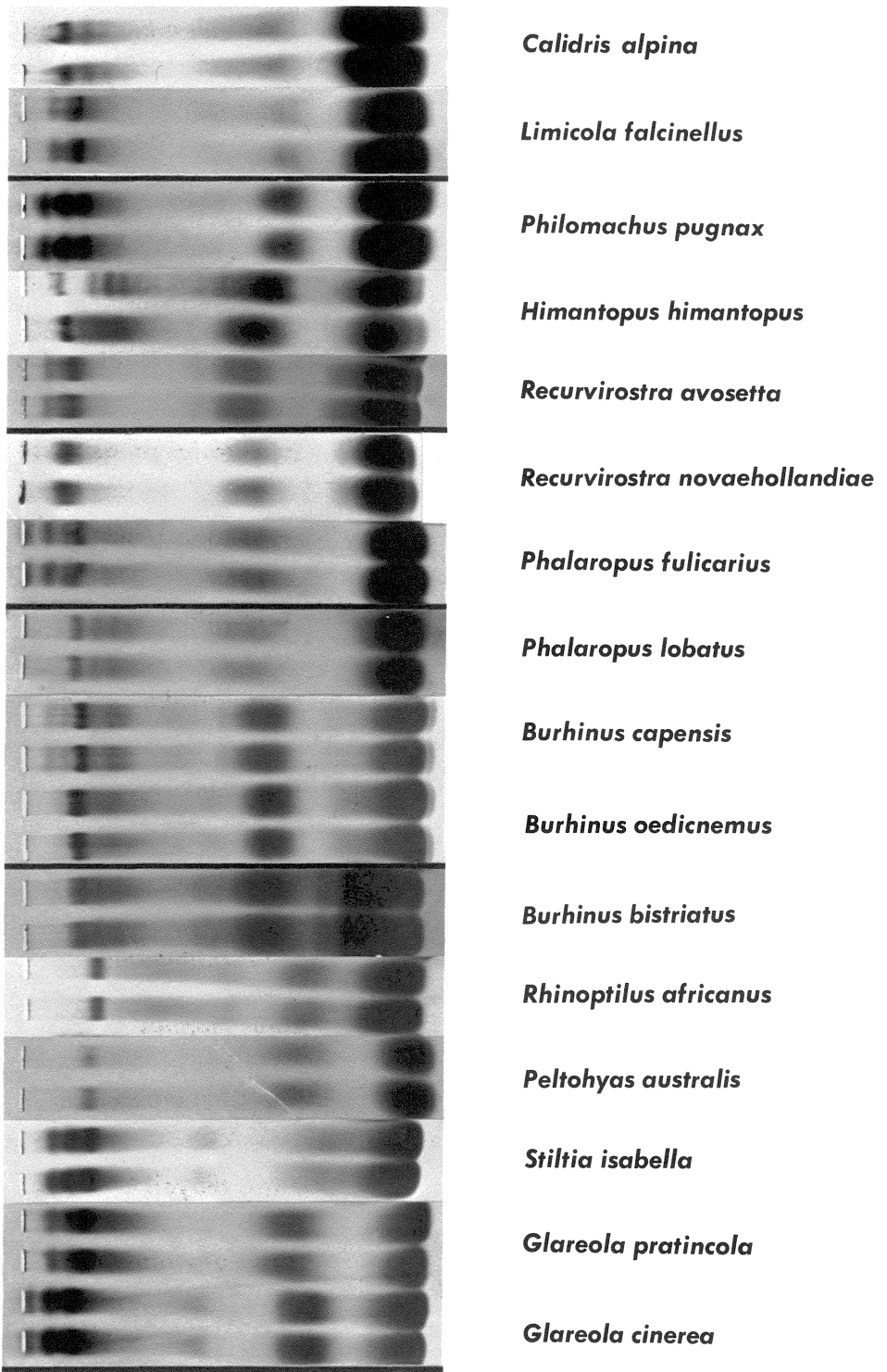
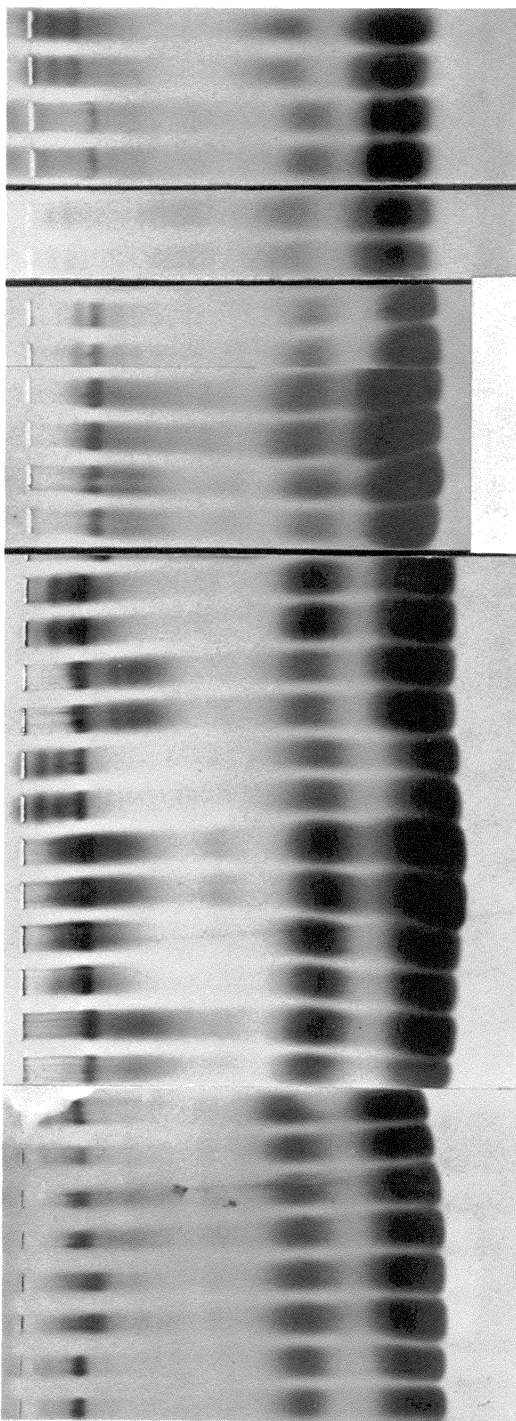


FIG. 22. Starch gel electrophoretic patterns of the Scolopacidae (part), Recurvirostridae, Phalaropodidae, Burhinidae, and Glareolidae.



Thinocorus orbignyianus

Attagis gayi

Chionis alba

Stercorarius skua

Stercorarius longicaudus

Stercorarius parasiticus

Larus tridactylus

Larus sabini

Larus atricilla

Larus pipixcan

Larus canus

Larus ridibundus

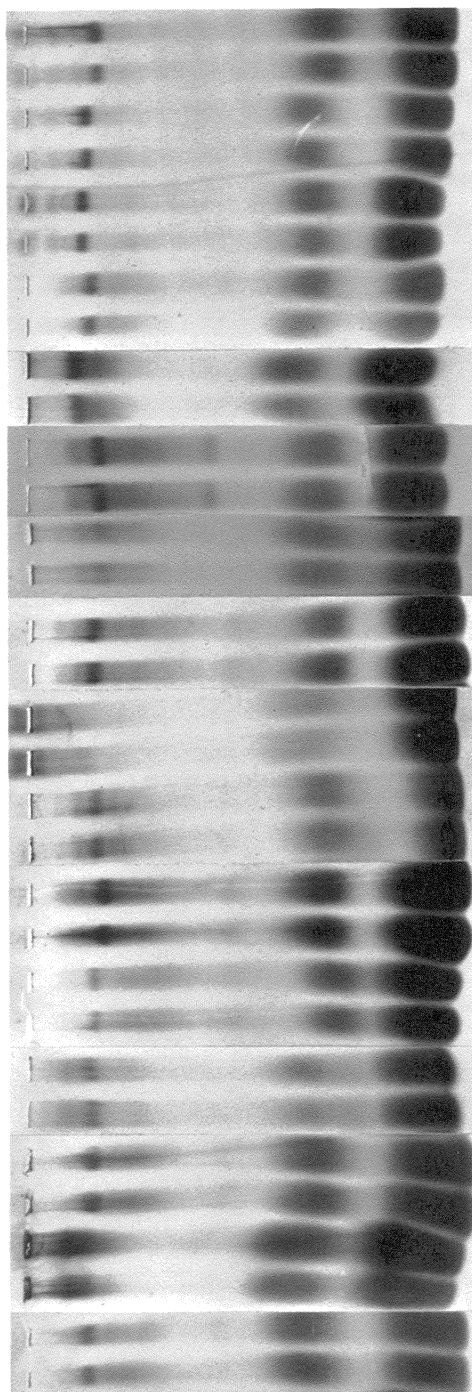
Larus marinus

Larus hyperboreus

Larus thayeri

Larus argentatus

FIG. 23. Starch gel electrophoretic patterns of the Thinocoridae, Chionididae, Stercorariidae and Laridae (part).



Larus fuscus

Larus dominicanus

Larus crassirostris

Larus delawarensis

Larus cirrocephalus

Rynchops nigra

Anous stolidus

Anous tenuirostris

Anous albus

Anous ceruleus

Sterna hybrida

Sterna nilotica

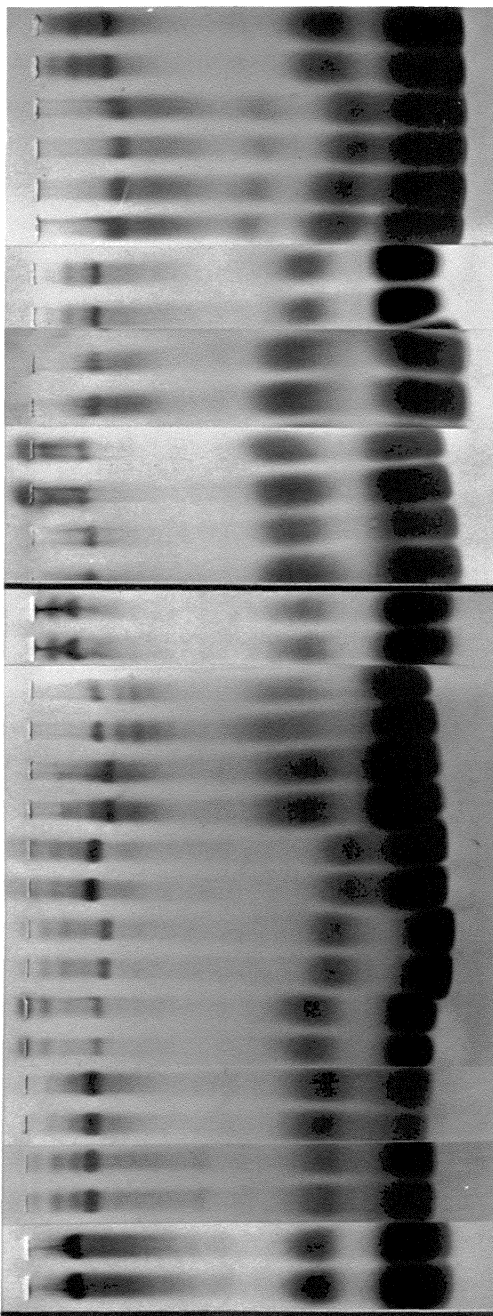
Sterna bergii

Sterna forsteri

Sterna dougallii

Sterna hirundo

FIG. 24. Starch gel electrophoretic patterns of the Laridae (part).



Sterna nigra

Sterna vittata

Sterna paradisaea

Sterna lunata

Sterna fuscata

Sterna albifrons

Sterna lorata

Plautus alle

Lunda cirrhata

Fratercula arctica

Alca torda

Cephus columba

Cephus grylle

Uria lomvia

Uria aalge

Uria aalge

FIG. 25. Starch gel electrophoretic patterns of the Laridae (part) and Alcidae.

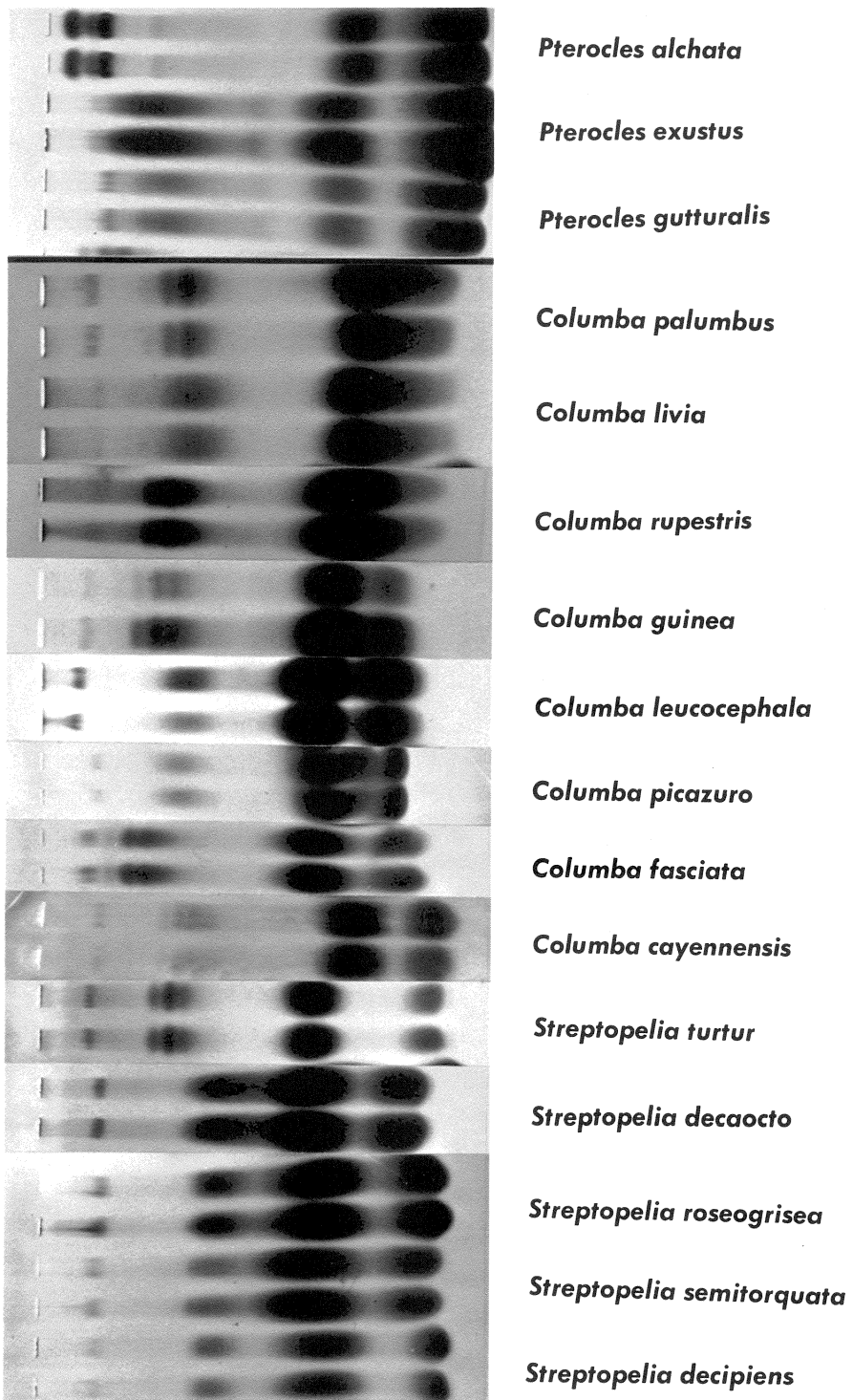
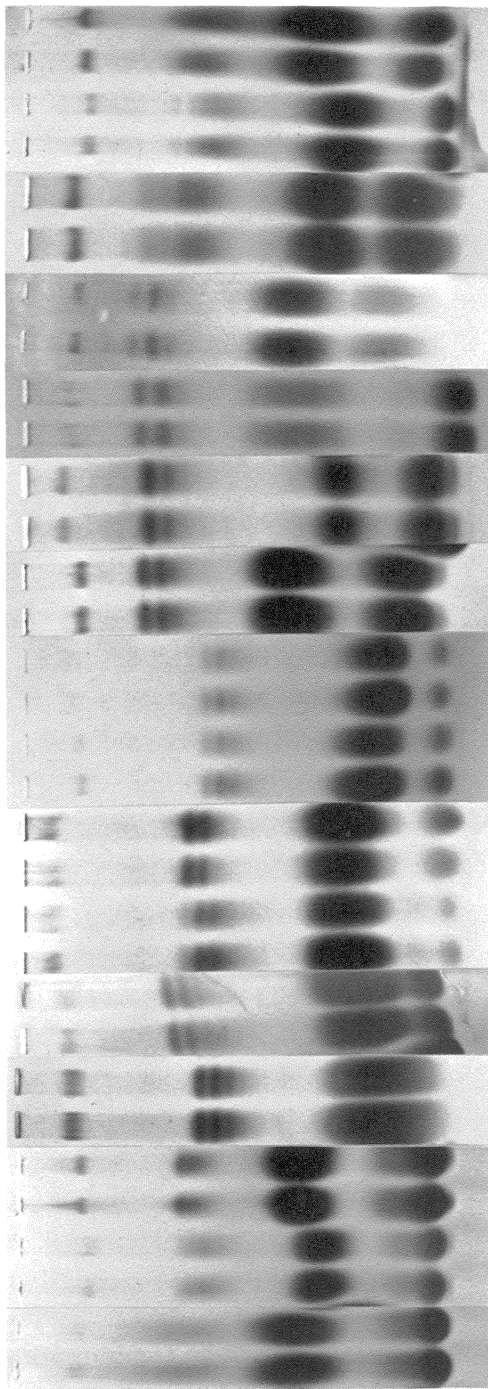


FIG. 26. Starch gel electrophoretic patterns of the Pteroclididae and Columbidae (part).



Streptopelia chinensis

Streptopelia capicola

Streptopelia senegalensis

Aplopelia larvata

Turtur chalcospilos

Oena capensis

Chalcophaps indica

Phaps elegans

Phaps chalcoptera

Ocyphaps lophotes

Petrophassa ferruginea

Geopelia striata

Leucosarcia melanoleuca

Zenaidura macroura

Zenaidura auriculata

Zenaida asiatica

FIG. 27. Starch gel electrophoretic patterns of the Columbidae (part).

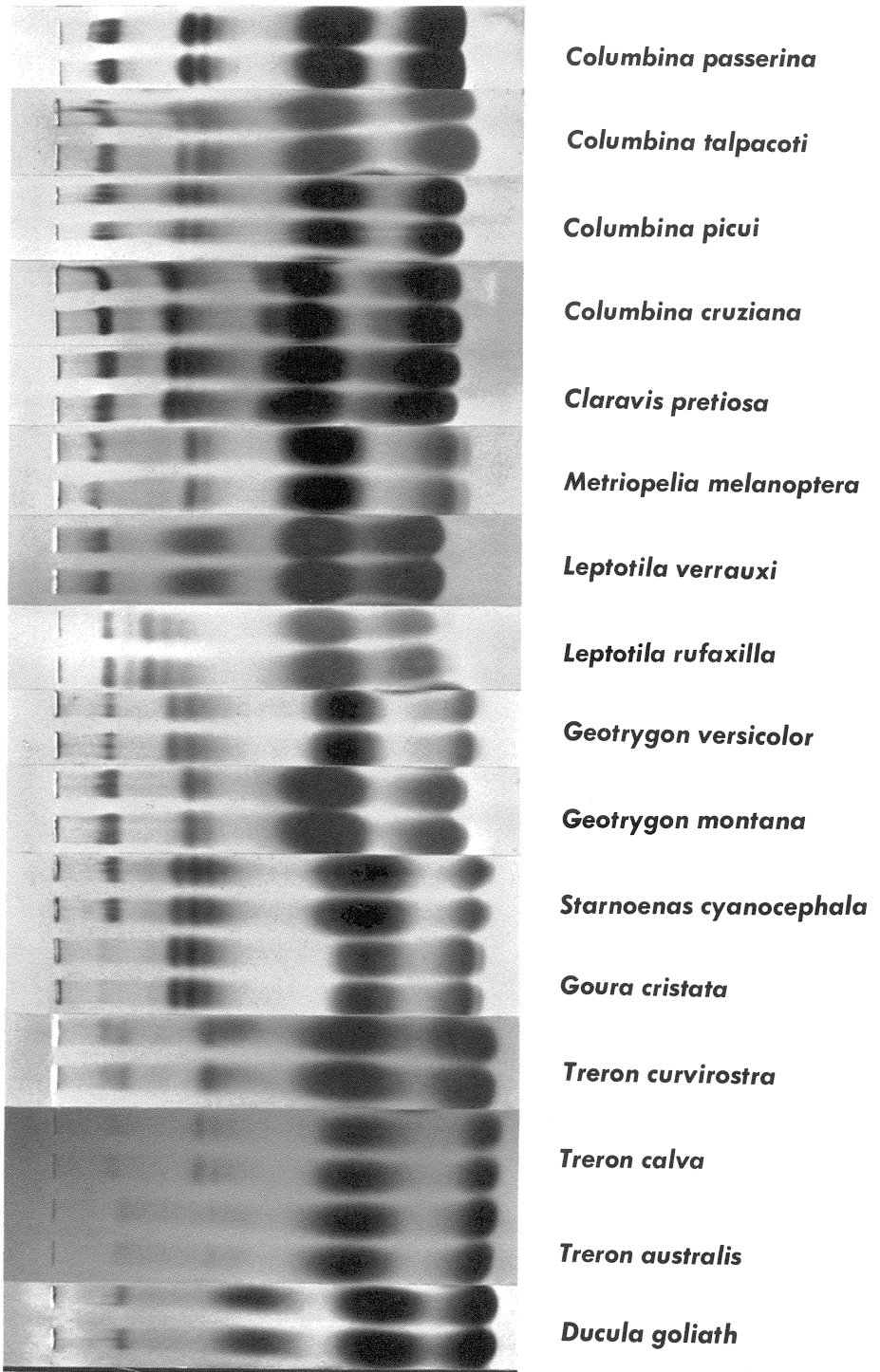
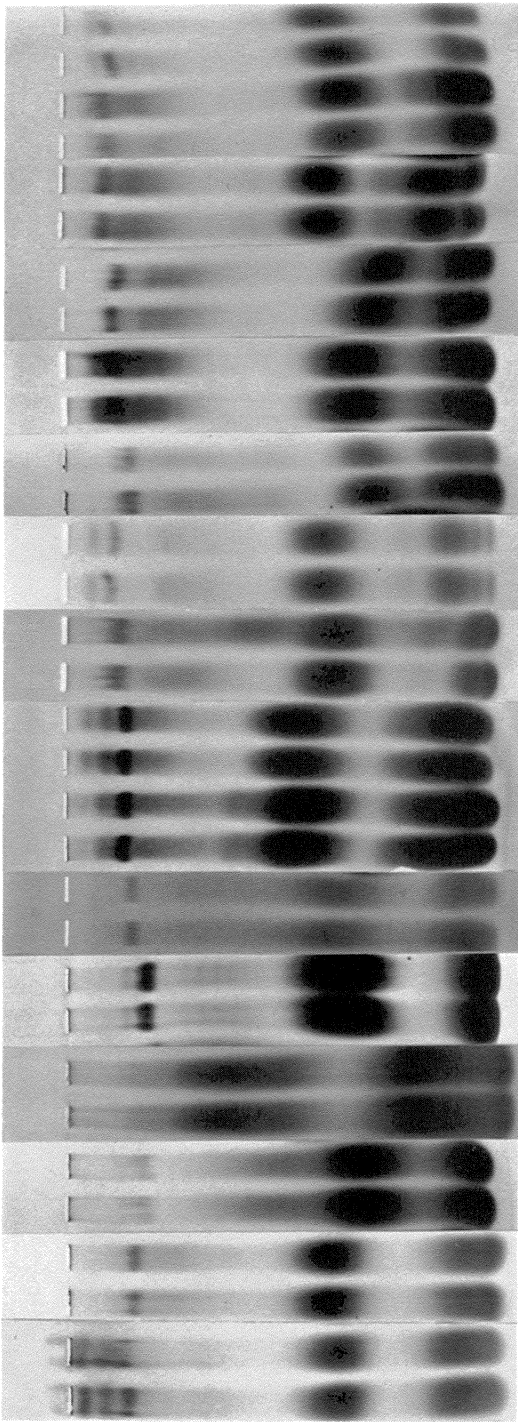


FIG. 28. Starch gel electrophoretic patterns of the Columbidae (part).



Calyptorhynchus magnificus

Calyptorhynchus baudinii

Calyptorhynchus baudinii

Cacatua tenuirostris

Cacatua roseicapilla

Nymphicus hollandicus

Aratinga mitrata

Aratinga canicularis

Amazona viridigenalis

Amazona autumnalis

Amazona ochrocephala

Psittacus erithacus

Lorius roratus

Psittacula columboides

Polytelis anthopeplus

Polytelis alexandrae

FIG. 29. Starch gel electrophoretic patterns of the Psittacidae (part).

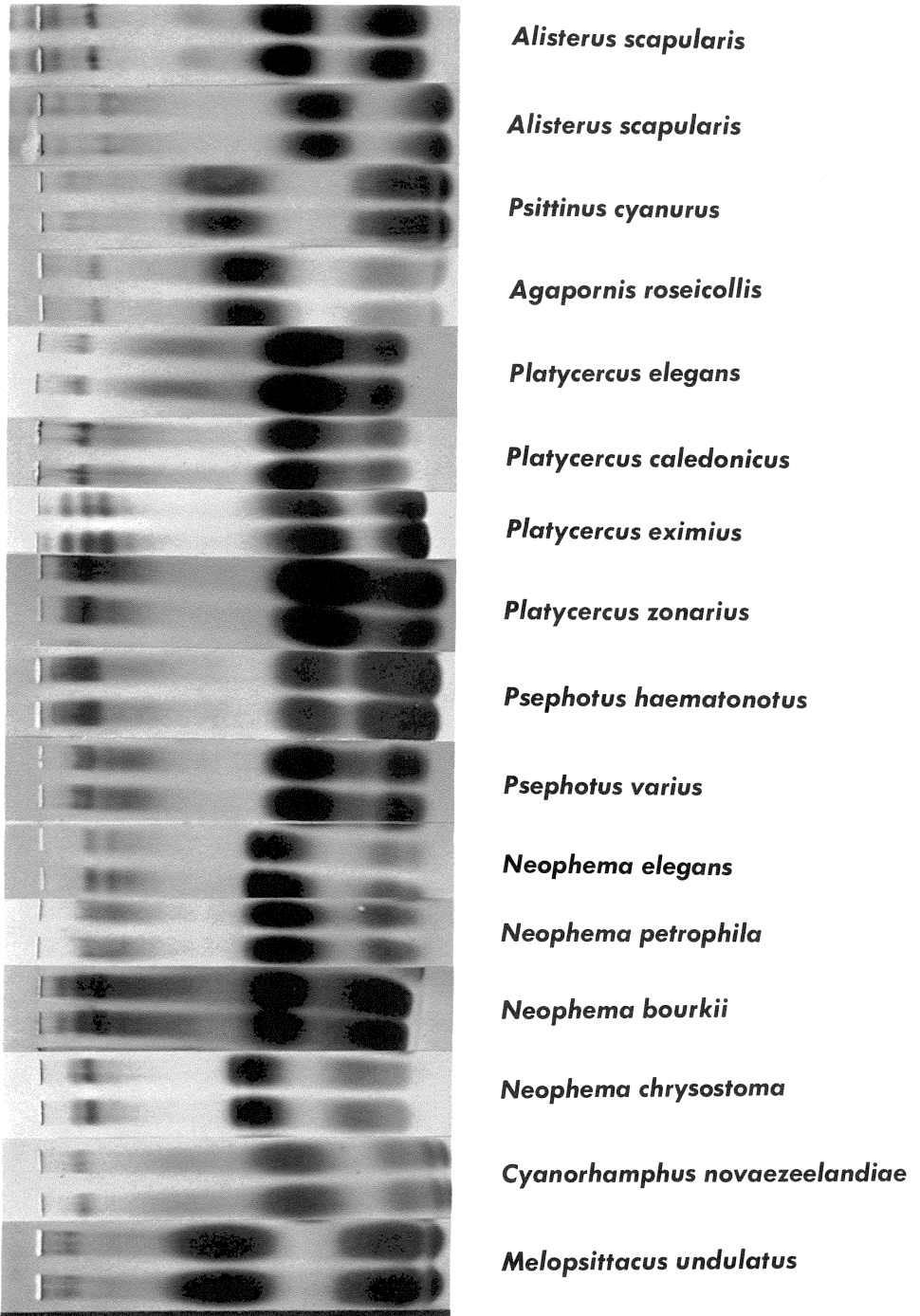


FIG. 30. Starch gel electrophoretic patterns of the Psittacidae (part).

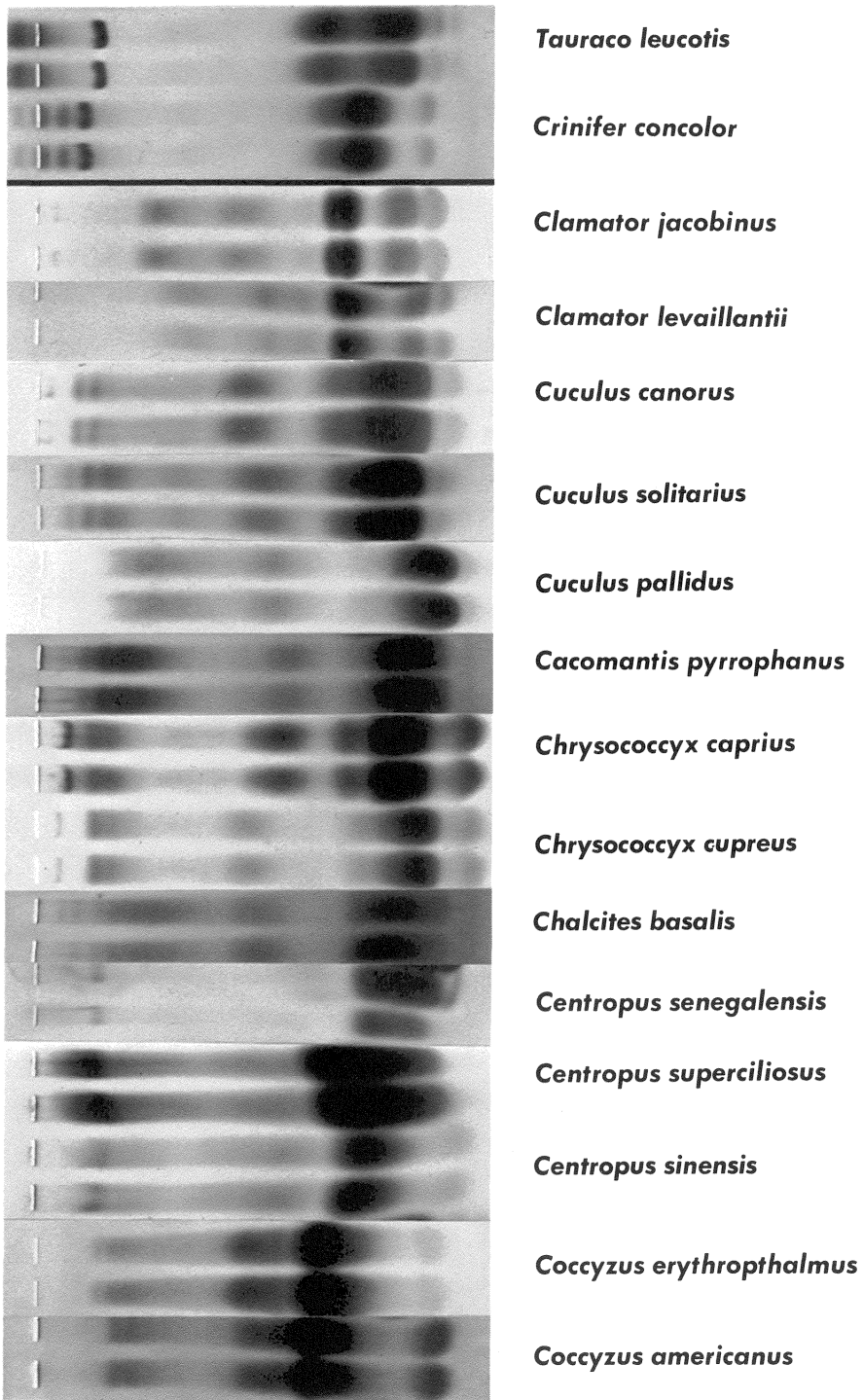


FIG. 31. Starch gel electrophoretic patterns of the Musophagidae and Cuculidae (part).

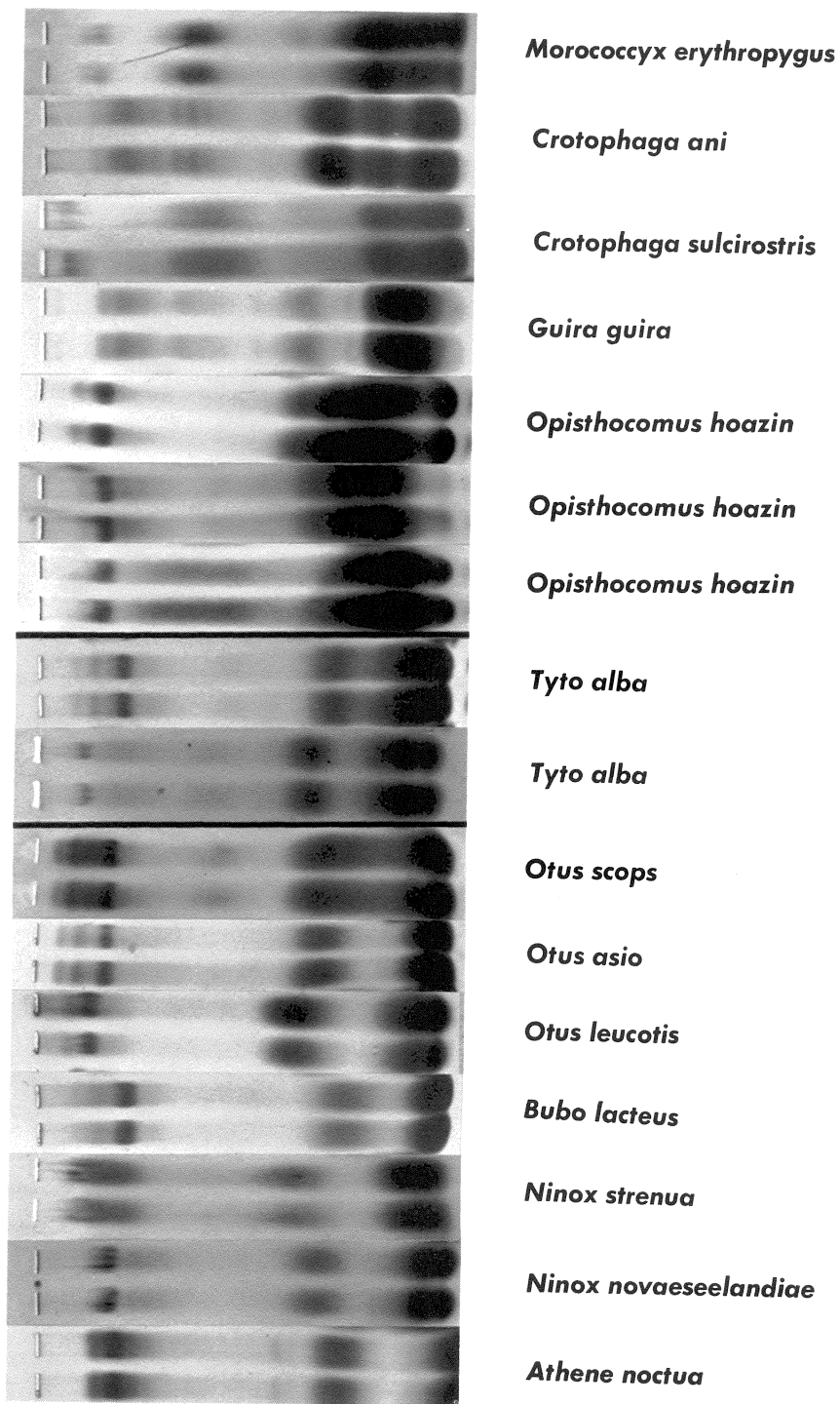


FIG. 32. Starch gel electrophoretic patterns of the Cuculidae (part), Tytonidae, and Strigidae (part).

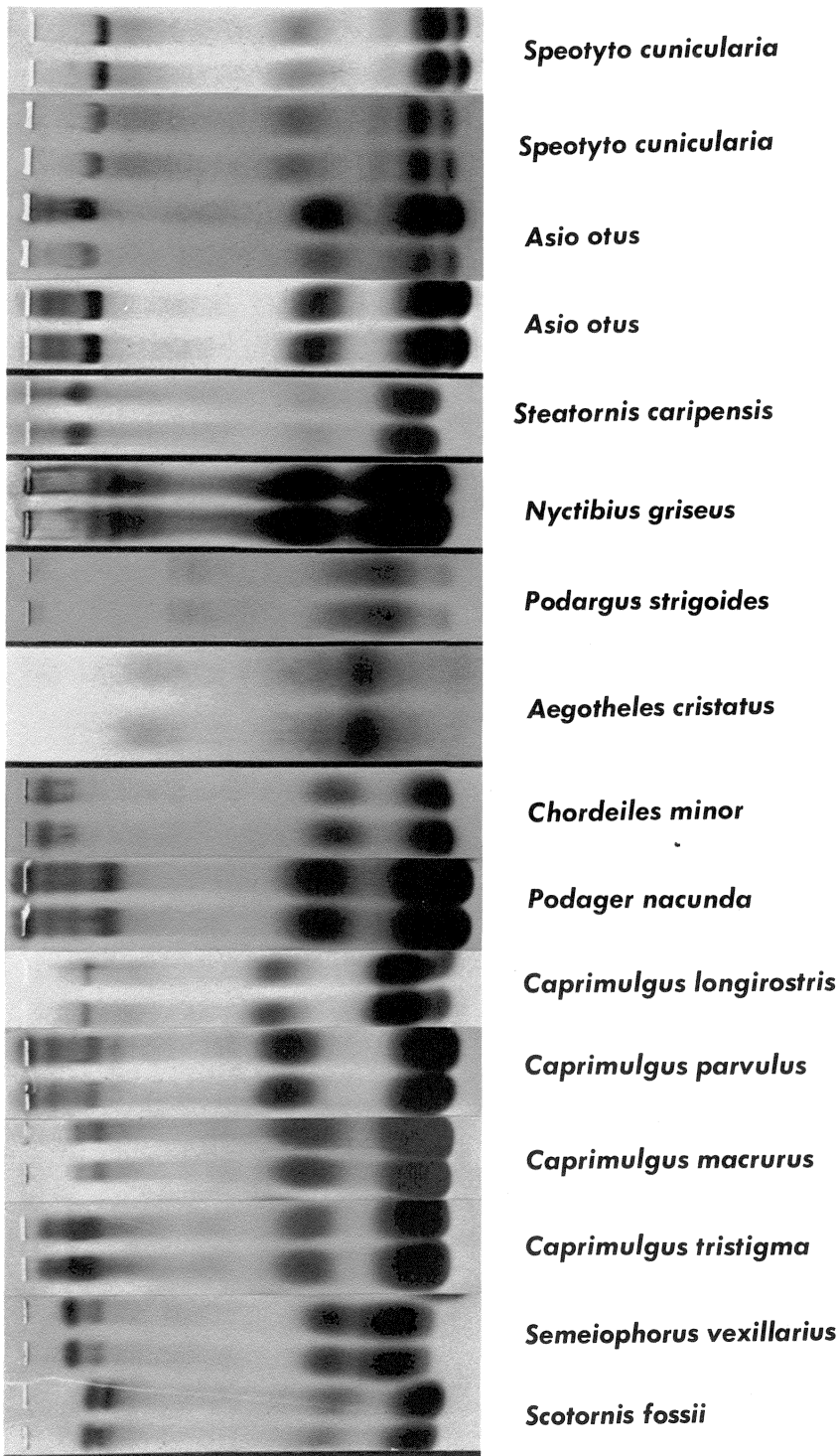


FIG. 33. Starch gel electrophoretic patterns of the Strigidae (part), Steatornithidae, Podargidae, Nyctibiidae, Aegothelidae, and Caprimulgidae.

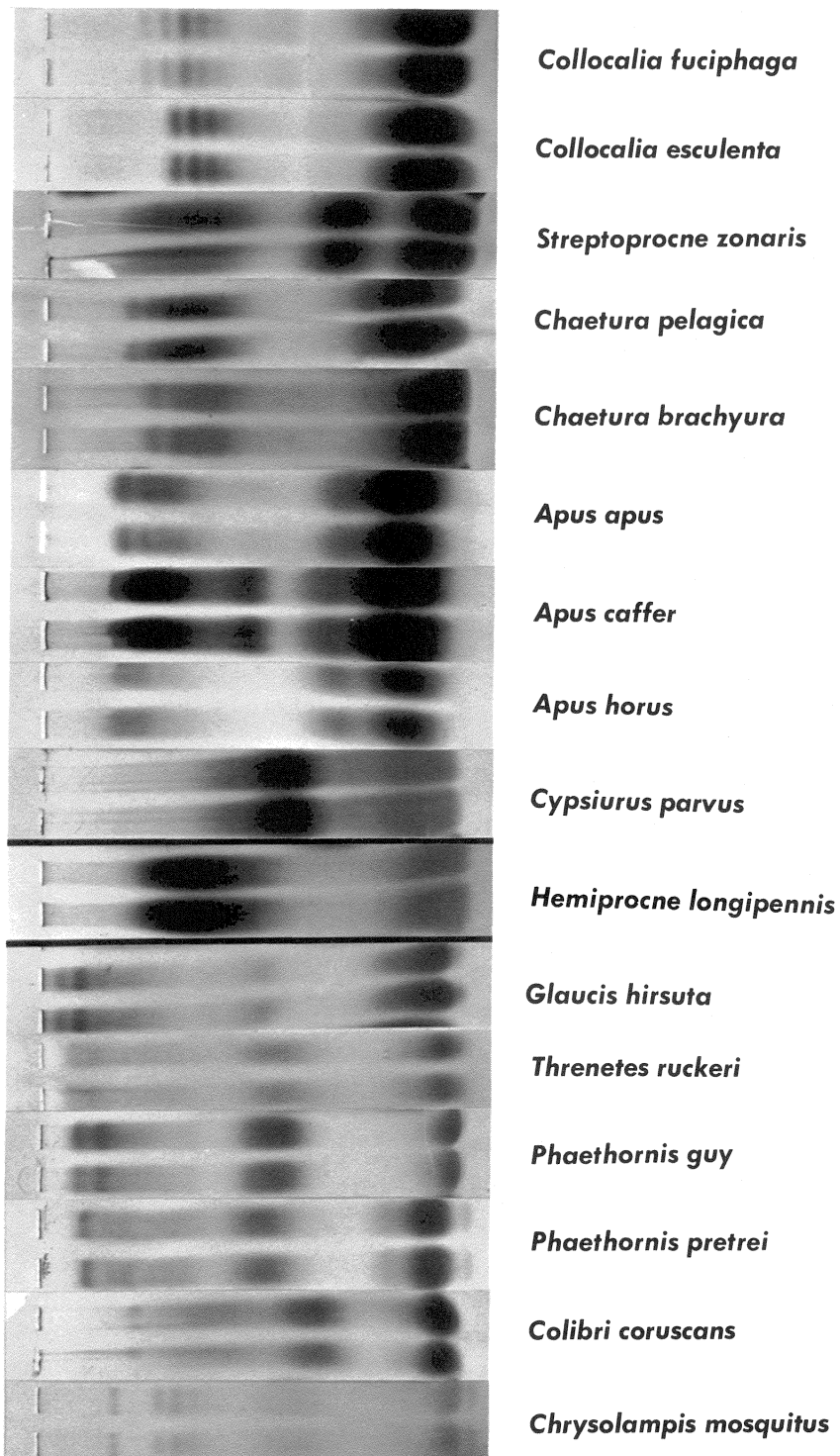


FIG. 34. Starch gel electrophoretic patterns of the Apodidae, Hemiprocnidae, and Trochilidae (part).

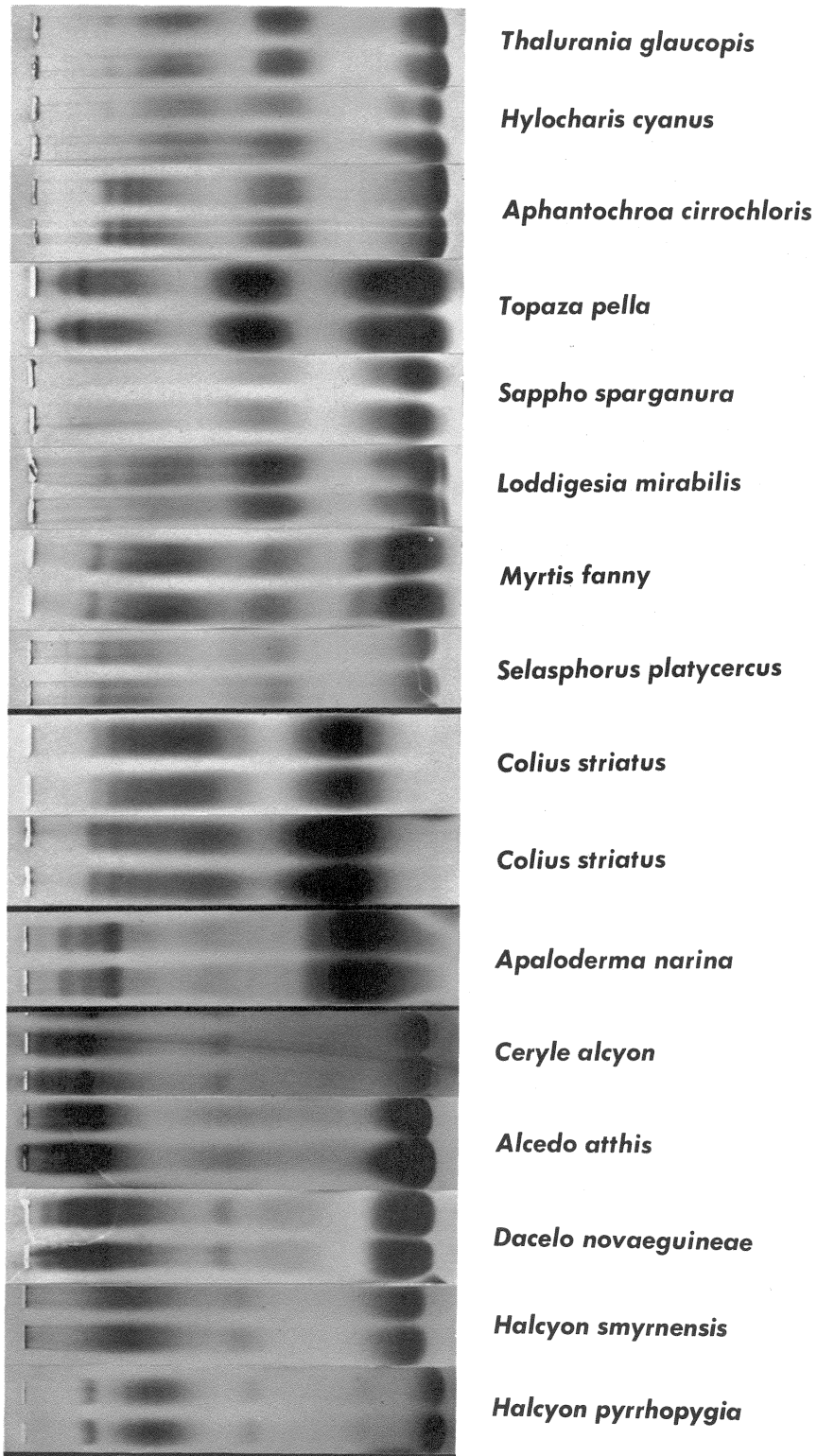


FIG. 35. Starch gel electrophoretic patterns of the Trochilidae (part), Coliidae, Trogonidae, and Alcedinidae.

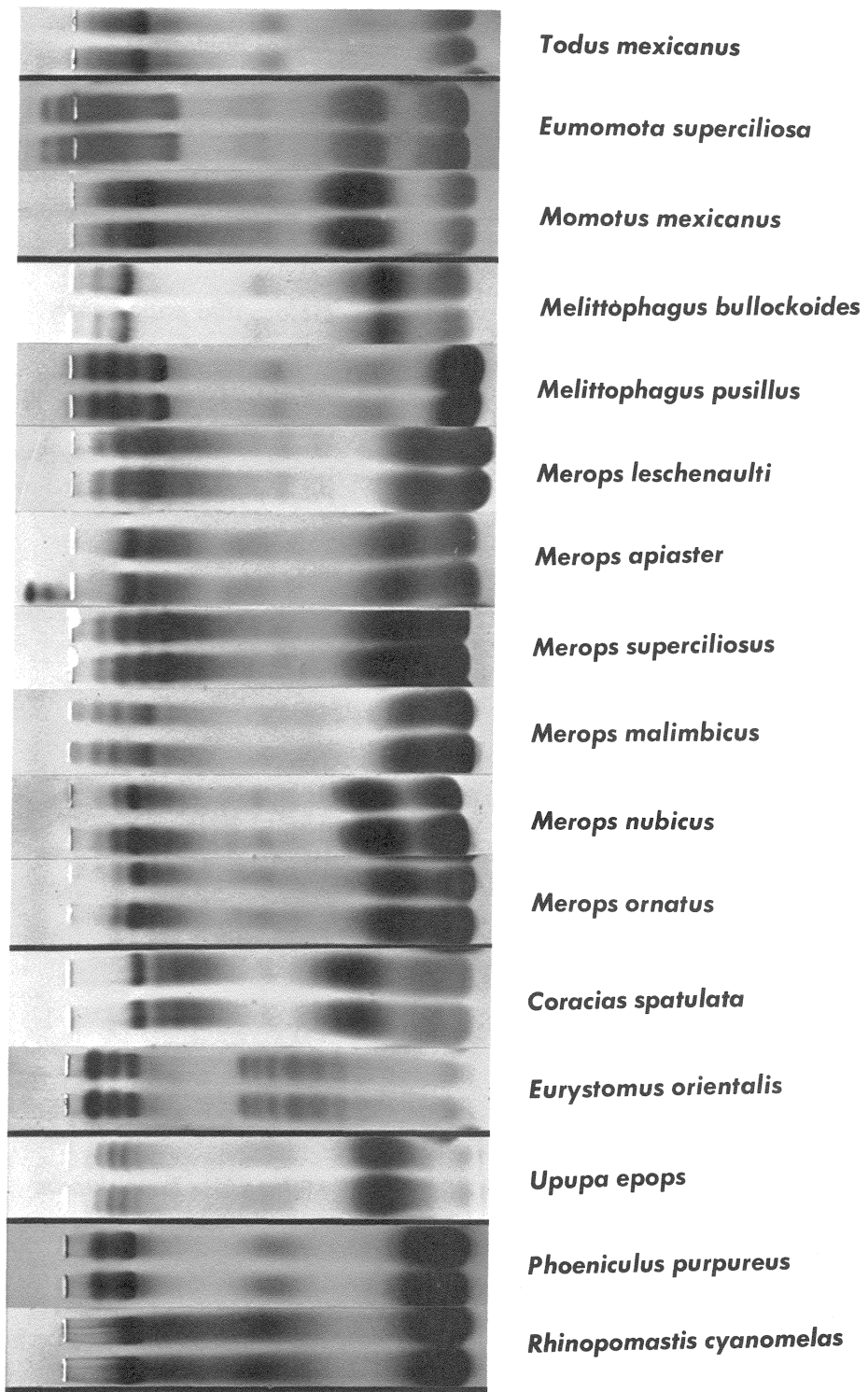


FIG. 36. Starch gel electrophoretic patterns of the Todidae, Momotidae, Meropidae, Coraciidae, Upupidae, and Phoeniculidae.

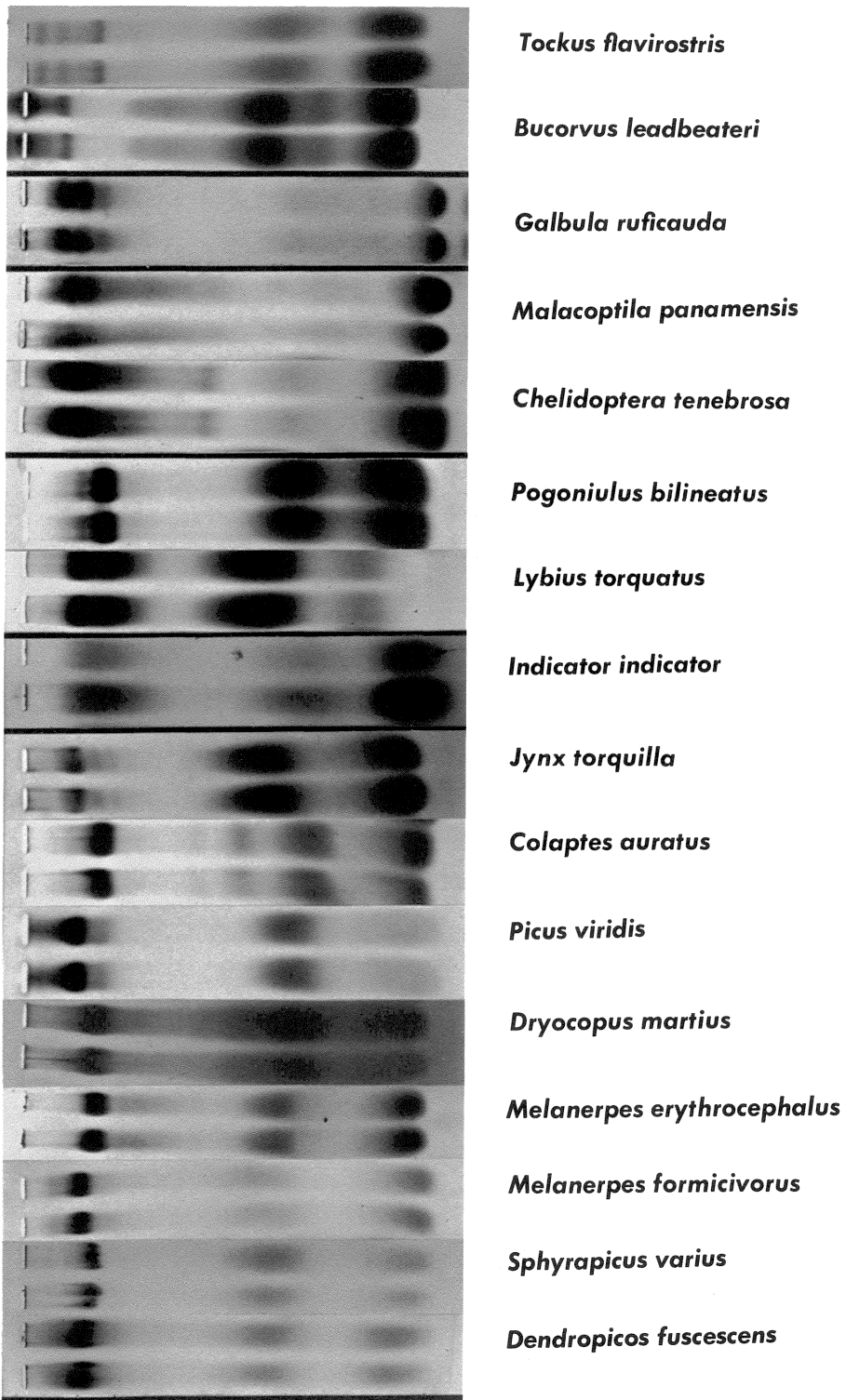


FIG. 37. Starch gel electrophoretic patterns of the Bucerotidae, Galbulidae, Bucconidae, Capitonidae, Indicatoridae, and Picidae.