TOWARD A PHYLOGENETIC CLASSIFICATION OF THE RECENT BIRDS OF THE WORLD (CLASS AVES)

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ABSTRACT.—This paper proposes that avian classifications should express the content of natural groups, that is, taxa that are our best estimates of genealogically related groups of species. The information content of classifications consists only of the hierarchical arrangement of groups within groups, and phylogenetic classifications can store and retrieve such information precisely because genealogical relationships are hierarchical in their logical structure. Present avian classifications, to the extent that they are based on overall (phenetic) similarity or on elevating morphologically distinct taxa to ranks higher than those of their close relatives, do not allow information about natural groups to be stored and retrieved unambiguously.

This paper is a first attempt at a phylogenetic classification of the higher taxa of Recent birds. Most currently recognized orders and families are probably monophyletic (with the exception of some family-rank taxa in the Passeriformes), but present classifications do not adequately express the interrelationships of these groups. Twenty orders are here classified into nine Divisions: Division 1 contains the Sphenisciformes, Gaviiformes (including grebes), Procellariiformes, and Pelecaniformes; Division 2 the Palaeognathiformes; Division 3 the Ciconiiformes and Falconiformes (including owls); Division 4 the Anseriformes and Galliformes; Division 5 the Gruiformes, Charadriiformes, and Columbiformes; Division 6 the Psittaciformes; Division 7 the Cuculiformes; Division 8 the Caprimulgiformes and Apodiformes; and Division 9 the Piciformes, Coliiformes, Coraciiformes, and Passeriformes. The families of each order are arranged into taxa that seem best to express our current knowledge of their phylogenetic relationships. *Received 26 November 1980, accepted 12 May 1981.*

HISTORICALLY, biological classifications have existed to convey knowledge about the structure of nature. With few exceptions natural historians have recognized that the knowledge to be specified in classifications concerns the identity of what are called *natural groups*. Indeed, it is the search for natural groups that has stoked the passions of countless biologists since the time of Aristotle. There have been, and continue to be, differences of opinion as to what exactly is meant by naturalness, but a general consensus has emerged, one that can be said to apply to pre- as well as to post-evolutionary times: a classification is natural to the extent that it conveys knowledge about the hierarchical structure of nature. This conception of natural classification represents the basic historical theme of biologists' attempts to classify; in modern systematic biology arguments exist over alternative conceptions of the hierarchical structure to be expressed in classifications, not over whether the structure of nature is hierarchical. Thus, knowledge about the heirarchical structure of nature can be specified either by a branching diagram or by a Linnaean classification: it does not really matter which, because each depicts the set membership of the included taxa.

This paper adopts a view of natural classification that has existed, to one degree or the other, within biology for nearly 200 yr: the hierarchy of nature consists of groups within groups, produced as a result of genealogical descent. The purpose of a natural classification, therefore, is to express our current state of knowledge about the genealogical relationships of taxa.

THE LOGICAL STRUCTURE AND INFORMATION CONTENT OF CLASSIFICATIONS

As implied above, the knowledge, or information, contained in branching diagrams or in Linnaean classifications is the same; it is the arrangement of groups within groups. This isomorphy in information content between branching diagrams and classifications has not always been recognized or accepted by systematists, and this has led to extended, unnecessary discussion and debate in the systematic literature. Because it has an obvious bearing on the scientific content of avian classifications, and because it will be illustrated repeatedly later, this relationship needs further amplification (see also Nelson 1972, 1973; Cracraft 1974a; Farris 1977; Wiley 1979; Eldredge and Cracraft 1980; Nelson and Platnick 1981).

Linnaean classifications consist of taxa (species or groups of species) placed in various taxonomic categories (genera, families, etc.). The logical structure of Linnaean classifications is such that taxa can be classified by subordination, that is, inclusion in another taxon of higher categorical rank, or they can be listed in a sequence with one or more taxa of equal rank (see Nelson 1973, Eldredge and Cracraft 1980: 165–171). Given this, a Linnaean classification can specify only the set-membership of its included taxa. In other words, Linnaean classifications do not necessarily contain intrinsic information about phylogenetic relationships or about genetic or morphological similarity, only about the hierarchical structure of groups within groups. So if biologists are to speak of the information content of classification, then the latter must be the set-membership of taxa.

Systematists compare taxa, and, using some similarity relationship, they cluster these taxa into sets that are then classified according to some criterion. There are alternative methods for comparing and clustering taxa, the most well-known being embodied in the systematic philosophies of numerical taxonomy (phenetics), evolutionary systematics, and phylogenetic systematics (cladistics). If the sole information content of a classification is its set-membership, then it is logical to conclude that the maximum amount of information for a given classification is obtained if the set-membership retrieved from that classification precisely reflects that of the clustering methods that were originally used to form the classification.

Cladistic hypotheses can be interpreted as hypotheses of genealogical relationships. Taxa are clustered on the basis of synapomorphies (Hennig 1966), and the taxa so formed are postulated to be strictly monophyletic. Cladistic hypotheses (cladograms) are hierachical in structure, and, whereas an analysis of derived similarity is used to form these hypotheses, the latter do not, in themselves, contain any exact information about the nature of those similarities, only that a pattern of nested synapomorphy is assumed to be present (see Eldredge and Cracraft 1980, Nelson and Platnick 1981). What cladograms do contain is a hypothesis of set-membership (presumably describing the genealogical hierarchy), and this can be classified within a Linnaean system. More important, if classified so as to preserve that set-membership, then the original cladistic hypothesis can be retrieved precisely from the classification: there is an isomorphy between the original genealogical hypothesis and the classification in terms of the sets of taxa that are recognized. In this sense, then, phylogenetic classifications constitute hypotheses about the structure of nature: they are repositories of our knowledge about the membership of natural (genealogical) groups.

ARE AVIAN TAXA NATURAL?

Virtually all those concerned with the construction of avian classifications would probably agree that knowledge of genealogical relationships is the major component of any classificatory scheme. It has been common practice among avian systematists, however, to ignore genealogy under certain circumstances. Nevertheless, if the scientific content of avian classification is to be measured according to some standard, the present state of our knowledge of avian phylogeny would seem to be the most important criterion. We might ask, therefore: to what extent are avian taxa natural?

It is remarkable that, with the possible exception of several popular presentations, there has been no comprehensive attempt to present a phylogenetic hypothesis of the higher avian taxa since that of Fürbringer (1888). To be sure, there have been numerous classificatory schemes proposed since then, and these obviously imply some phylogenetic content. However, because these classifications are not avowedly phylogenetic, that is, because the hierarchical arrangement of taxa does not necessarily specify concepts of genealogy, these classifications poorly express hypotheses of avian history.

It is my view that most avian orders (say, of Mayr and Amadon 1951, or of Wetmore 1960) are monophyletic, but that most hierarchical arrangements of taxa within orders are not. The reasons for this are not difficult to identify (Cracraft 1972, 1980): it has resulted from the attempts of avian systematists to cluster taxa on the basis of overall (or weighted) similarity and to bestow high rank on taxa that are morphologically divergent compared to their closest relatives. More specifically, systematists have not partitioned similarity into its primitive and derived components and clustered using only the latter. Because a distinction is not made between primitive and derived characters, the analysis of different anatomical systems frequently has produced conflicting opinions about relationships. Such conflicts are often so pronounced that some workers have viewed the situation as hopeless; Stresemann's (1959) rationalizations and classification are the epitome of this viewpoint, but evidence of it can be found in virtually every classification. A cladistic analysis can help resolve this conflict by showing that at least some of the confusion is the result of uniting taxa on the basis of primitive characters (see discussion of Pelecaniformes, below). This is not to say, of course, that every cladistic analysis applied to the same group will always produce either identical results or a fully resolved phylogenetic hypothesis, but at least the reasons for any differences of opinion will be easy to identify (see Eldredge and Cracraft 1980, for a general discussion of such conflicts).

THE INFORMATION CONTENT OF AVIAN CLASSIFICATIONS

Because the information content of a classification resides in its expression of group membership, it follows that the extent to which a classification contains information is proportional to the complexity of its hierarchical structure: the more complex that structure, the more information about group membership.

Historical trends in the degree to which avian classifications express information content are not readily apparent. Some 19th century classifications contain very little information about group membership; others are quite complex (e.g. Stejneger 1885, Fürbringer 1888). Among more recent classifications, that of Mayr and Amadon (1951) shows little complexity in its treatment of the nonpasseriforms but a great

deal in its arrangement of the passerines. The classification of Wetmore (1960) is very nearly the opposite, being complex for the nonpasserines but exceedingly simple for the passeriforms. The nonpasseriform classification of Verheyen (1960), despite its idiosyncrasy, is nevertheless fairly complex in information content, and the classification of Storer (1971) resembles that of Wetmore in its complexity.

One obvious goal of avian classifications is to express as much information about group membership as possible. Thus, a major effort should be expended to resolve the hierarchical structure of avian taxa and to express that in classifications. Classifications without much structure are simply uninformative and of little scientific merit.

THE IMPORTANCE OF PHYLOGENETIC CLASSIFICATIONS

A large literature exists on the characteristics and advantages of phylogenetic classifications as compared to those constructed by the methods of numerical taxonomy or classical evolutionary systematics. Phylogenetic classifications have been shown to be more efficient for the storage and retrieval of information about natural groups and, as a result, as more efficient at predicting the group membership distributions of newly analysed characters or taxa (see, for example, Farris 1977, 1979a, 1979b; Mickevich 1978; Platnick 1978; Wiley 1979; Nelson 1979; Eldredge and Cracraft 1980; Nelson and Platnick 1981).

Avian classifications traditionally have been constructed following principles that could be categorized under the rubric of classical evolutionary systematics (e.g. Simpson 1961, Mayr 1969). Although these classifications have not ignored our changing views of natural groups, certain methods of ranking taxa have prevented avian classifications from expressing concepts of natural groups. In particular, the elevation of distinctive taxa to a rank higher than that of their closest relatives, the delimitation of boundaries of taxa according to their size, and attempts at achieving a "balance" in the categorical rank of taxa within related groups not only lead to the recognition of nonmonophyletic taxa (in this case, mainly paraphyletic), they also lower the information content, predictability, and complexity of the classifications (see above citations). Ironically, the purpose behind these "criteria" of ranking (Mayr 1969) is to emphasize some conception of morphological or "adaptive" uniqueness, but as Farris (1977) and Eldredge and Cracraft (1980) have argued, the methods of ranking employed by evolutionary systematists completely vitiate their professed goals.

It can be suggested that ornithology has not fully appreciated the scientific importance of classifications. Instead, emphasis has been placed on maintaining the stability of contemporary systems. What is lost in this view is that classifications— particularly if they are phylogenetic—are scientific statements about the organization of the natural hierarchy. And like any scientific statement, they should be subjected to continuous revision and change. The problem of stability is actually a matter of nomenclature, which is doubtfully within the realm of scientific inquiry. With respect to the scientific knowledge summarized by classifications, stability is neither to be admired nor encouraged (Gaffney 1979).

It is certainly true that names of taxa cannot be changed repeatedly without an adverse effect on communication. But the use of a phylogenetic system does not necessarily imply major changes in categorical rank or the introduction of numerous new taxon names, as some critics have claimed (see Eldredge and Cracraft 1980,

for a discussion of this); the classification proposed below will help dispel many of these criticisms. Despite the fact that many radically different avian classifications have been proposed during the last century, scientific progress within ornithology does not seem to have suffered.

The use of phylogenetic classifications within ornithology will improve the content of avian systematics in general. These classifications will serve as more precise scientific hypotheses about the composition of natural groups, and accordingly will be open to more specific criticism, than have previous classifications. Phylogenetic classifications should also encourage new investigations at all levels of the hierarchy; because current classificatory schemes have been so influenced by vague concepts of ranking, their significance as organizers of the research program of avian systematics has been diminished. Phylogenetic classifications should change that: they provide a basis on which to organize all manner of observations within the realm of comparative biology.

A PHYLOGENETIC CLASSIFICATION OF BIRDS

In this section I present the first attempt at a phylogenetic classification of the higher taxa of birds. I view this classification as a preliminary expression of ideas that will certainly be modified and improved with future work. No aspect of the classification is viewed as being writ on stone.

At this point matters of explanation, and the obligatory *mea culpa,* are in order. I make no pretense about providing complete documentation for each systematic allocation, but I have tried to approach this problem from two standpoints. First, many of the reasons for these decisions are based on published or soon to be published studies, but in the case of the latter work I have cited them only if they are parts of manuscripts that will be published in the very near future. Second, for those decisions that are based on little evidence or merely follow tradition, I have specifically made note of this. It is too early to document a complete phylogeny of birds, and thus I have tried to call attention to areas of controversey and systematic questions in need of more study. I have not consciously ignored contemporary opinions that are at variance with my views. All in all, I believe that this classification is as well documented, if not better, as any classification proposed in recent years.

The classification attempts to maintain traditional names and ranks for the various taxa to the extent possible. Two problems within ornithology have been the tendency to conceptualize groups of taxa as being "orders" or "families" and to assume that certain morphological or behavioral distinctions are worth ordinal or familial rank. This type of thinking has hurt avian systematics for reasons already mentioned. A final decision about the relative ranks of avian taxa will have to await the integration of avian phylogenetic results with those of the other vertebrates and an eventual classificatory scheme for all these taxa.

Because phylogenetic classifications embody more information content and are more complex than traditional classifications, it has been necessary to introduce additional categorical levels (e.g. divisions, cohorts) not usually found in recent classifications. Virtually all of these categorical levels, however, have been used in previous avian classifications or are common in those of other vertebrates. It will be evident that the introduction of these levels increases the information content of the classification. I have chosen not to name formally the taxa classified at the categorical level of division, because in a number of cases their status as monophy-

letic groups is not yet well documented. Nevertheless, it is important to propose preliminary hypotheses of interordinal relationships, if only to provide the basis for future critical discussion, and this represents a departure from nearly all recent classifications in which no attempt is made to express relationships at this level.

DIVISION 1: ORDERS SPHENISCIFORMES, GAVIIFORMES,
PROCELLARIIFORMES, PELECANIFORMES

The detailed evidence supporting the relationships depicted in this classification is presented in three papers (Cracraft in press, MS; Manion and Cracraft MS). These four orders have often been placed near one another, although a strong argument for their interrelationships has not yet been made. A cladistic analysis of their skeletal morphology has clarified these relationships to a considerable degree.

Evidence for a sister-group relationship between the Gavio-impennes on the one hand and the Stegano-tubinares on the other is admittedly weak. At this time, the main reason for including them together is the general overall similarity of their cranial anatomy (Cracraft MS). Immunological studies are generally consistent with the hypothesis that this water-bird complex forms a natural group (Ho et al. 1976). This relationship needs further investigation.

The spherisciforms and gaviiforms (including grebes) share a number of similarities not found in other birds (Cracraft in press), including characters of the skull, sternum, and pelvis (the skeletal elements of the wings and hindlimbs of penguins are so highly modified as to be not readily comparable with other birds). Immunological data also support this relationship (Ho et al. 1976). Penguins have frequently been allied with procellariiforms on the basis of Simpson's (1946) study of fossil penguins, but, other than a speculative scenario about how penguins might have evolved from flying ancestors, little supporting evidence was presented.

There are strong reasons based on skeletal anatomy to consider procellariiforms and pelecaniforms to be sister-groups (Cracraft MS). For example, in cranial morphology the primitive procellariiforms (diomedeids) and primitive pelecaniforms (especially fregatids) are exceedingly similar, but the shared characters extend to the postcranial skeleton as well.

It has been traditional to place grebes and loons in separate orders, and most recent authorities have considered them to be unrelated and their similarities convergent. As was pointed out by numerous 19th century systematists, however, the two groups are exceedingly similar, and these similarities can be interpreted as derived within birds (Cracraft in press). Related to the loons and grebes are the Cretaceous diving birds, *Enaliornis, Hesperornis, Neogaeornis,* and *Baptornis.*

Within the Procellariiformes the albatrosses are the sister-group of the other members of the order (Manion and Cracraft MS). The diomedeids are primitive in morphology compared to the hydrobatids and procellariids and many of these primitive characters can be postulated to be derivative at a higher hierarchical level that also includes the Pelecaniformes (Cracraft MS). The Hydrobatidae and Procellariidae are united on the basis of possessing a presphenoid sinus in which the posteroventral portion of the lateral wall (just dorsolateral to the stapes) develops a bony ring. The procellariids, including *Pelecanoides,* comprise a monophyletic group defined by an expanded temporal fossa, basipterygoid processes, and an additional fenestra between the prootic foramen and the upper tympanic recess. The generic interrelationships within the procellariids have always presented problems.

Pelecanoides is traditionally placed in its own family, but only because systematists have given undue emphasis to its morphological distinctness; the genus seems clustered with *Puffinus, Procellaria,* and their allies, and thus its family designation should be abandoned (Manion and Cracraft MS).

An hypothesis of pelecaniform interrelationships was presented by Lanham (1947). A cladistic interpretation of the skeletal morphology generally confirms Lanham's phylogenetic hypothesis, with one major difference (Cracraft MS): the characters used to relate the tropicbirds and frigatebirds are primitive. The frigatebirds can be united with the pelecanids, sulids, and phalacrocoracids (including *Anhinga*) on the basis of derived characters including fused palatines, loss of the medial posterolateral processes of the sternum, and young that are hatched naked, among others.

Cottam (1957) suggested that the African Shoebill Stork (*Balaeniceps rex*) is actually a pelecaniform. This hypothesis was based primarily on the presence in *Balaeniceps* of some obviously derived characters that have counterparts in some pelecaniforms: fused palatines, prominent hook at the tip of the premaxilla, and a fusion of the furculum and sternum. Cottam's study has a major weakness in that the characters of *Balaeniceps* were not interpreted within the context of a phylogenetic (primitive-derived sequence) analysis of both the pelecaniforms and ciconiiforms. When this is done, it is apparent that characters of the Shoebill do not fit into the hierarchical pattern of derived characters shown by the pelecaniforms but that they do within the ciconiiforms (Cracraft MS; see Division 3 below).

DIVISION 2: ORDER PALAEOGNATHIFORMES

Most classifications of recent years have placed the ratites and tinamous in separate orders, considering them to be unrelated to one another (e.g. Mayr and Amadon 1951, Wetmore 1960, Storer 1971). Some workers during the first half of this century considered the ratites and tinamous to be related (e.g. Lowe 1928), but it was the paper by McDowell (1948), arguing that the palaeognathous palate could not be defined, that convinced many of their nonmonophyly. Thus, for example, prior to his revised classification in 1951, Wetmore placed the palaeognaths in the same superorder.

Lately the naturalness of the palaeognaths has gained widespread support. First, Bock (1963) argued strongly that the palaeognathous palate can be defined and hence can be used to support the monophyly of these groups. Then, Parkes and Clark (1966) showed that the rhamphothecal structure of the bill in the palaeognaths is unique within birds. Finally, in 1974 I postulated that the open ilioischiatic fenestra is a derived condition within birds and thus indicative of monophyly, and, using primitive-derived sequences in a large number of postcranial characters, I proposed a phylogeny for the group (Cracraft 1974b). To these studies one can add the information that the karyotypic structure (sex-determining system) of palaeognaths is apparently unique within birds (de Boer 1980). Furthermore, phenetic analyses of immunological distances (Prager et al. 1976) and DNA hybridization distances (Sibley and Ahlquist 1980, 1981) support the unity of the palaeognaths.

There have been two lines of evidence and reasoning opposed to the hypothesis of palaeognath monophyly. The first is that of Gingerich (1973, 1976), who argued that the characters used to define the palaeognaths are primitive and consequently "it is possible, even probable that the groups of living ratites and the tinamous are

paraphyletic" (1976: 32). I have commented elsewhere (1980) on certain aspects of the phylogenetic reasoning associated with this problem: even if the three characters noted above are primitive, that in itself does not constitute an argument against monophyly but merely signifies that the hypothesis of monophyly is not well corroborated. A hypothesis of nonmonophyly can be supported only by showing a relationship of one or more of the palaeognaths to other avian taxa, but this has not been done. At this point, then, we might ask what is the nature of the evidence that the palate, bill, and pelvic structures of palaeognaths are primitive?

Gingerich considered that *Hesperornis* was "clearly palaeognathous in all diagnostic features," and he defined the palaeognathous palate as one in which (1) the pterygoid and palatine are firmly joined, (2) palatines are separated from the sphenoid rostrum by the pterygoids, (3) strong basipterygoid processes are present, (4) the vomer is relatively large, and (5) the orbital process of the quadrate is involved in a complex pterygoquadrate articulation (1973: 72, 1976: 30). Because of its supposed presence in *Hesperornis,* he concluded that the palaeognathous palate is primitive within birds. I believe that a number of Gingerich's morphological interpretations are open to question and that the only way *Hesperornis* can be said to be palaeognathus is to accept these questionable interpretations and redefine the concept of palaeognathy, both of which Gingerich has done.

The reconstructed palate of *Hesperornis* is very different from the palaeognathous condition found in ratites and tinamous. Perhaps the most important characteristic of the palaeognathous palate, used by virtually all previous workers but not mentioned by Gingerich, is the typically strong *fusion* of the pterygoid-palatine-vomer articulation. The only exception is found in *Struthio* in which the vomer falls slightly short of the fused pterygoids and palatines, and in this case one can make a strong argument for this being a further derived condition within the ratites, as there is much corroborative evidence that *Struthio* and *Rhea* are closely related and are advanced within the palaeognaths (see below). *Hesperornis* did not possess this defining character. The vomer of *Hesperornis* is not enlarged much (*contra* Gingerich) and falls far short of the palatine-quadrate articulation. Unlike the condition of the palaeognaths, the pterygoids and palatines were not fused. Gingerich (1973: 71) describes the joint as being "relatively immovable" and the bones as "firmly joined, though not fused"; in other words, the joint appears to be typical of birds in general but decidedly unlike the condition in palaeognaths.

Like that of palaeognaths, the pterygoid of *Hesperornis* has a broad articulation with the quadrate, particularly with its orbital process (Gingerich 1976: 29, Fig. 3). *Hesperornis* also had an articulation between the pterygoid and the basipterygoid process of the basisphenoid. But this complex is not very similar to that of the palaeognaths. First, the pterygoid of *Hesperornis* is exceedingly different in shape, being very short and broad, whereas those of the palaeognaths are much larger and longer. In palaeognaths the basipterygoid articulation is close to the pterygoquadrate juncture—another characteristic of the palaeognathous palate (Bock 1963)—but in *Hesperornis* it is at the distal end (admittedly the peculiar shape of the pterygoid virtually necessitates this arrangement, but again it emphasizes the fact that *Hesperornis* is not that similar to the palaeognaths).

Finally, in all palaeognaths except some (all?) moas (Dinornithidae), the pterygoids and/or the fused vomer intervene between the palatines and the basisphenoid rostrum. Gingerich (1973: 72, 1976: 30) claims that *Hesperornis* possesses the palaeog-

nathous condition, but once more the concept of palaeognathy is redefined to suit his purposes: in *Hesperornis* the pterygoids are so *small* (not large as in palaeognaths) that in order to articulate with the pterygoids the palatines must extend posteriorly and "by-pass" the rostrum. This condition is not the palaeognathous condition; in *Hesperornis* the pterygoids do not intervene between the palatines and rostrum.

So I conclude, from Gingerich's own reconstructions, that the palate of *Hesperornis* is not palaeognathous. Moreover, the shapes of the palatines are so peculiar within birds (and thus they are not at all similar to palaeognaths) as to almost cast doubt on their identity. As reconstructed and figured (Gingerich 1973: 71, Fig. 1; 1976: 28, Fig. 2), they are long, very thin, and broaden only posteriorly near the pterygoid articulation: there appears to be very limited space on them for the retractor musculature (Gingerich's arguments that *Hesperornis* did not have the typical avian prokinesis are unconvincing). The palate of *Hesperornis* needs to be reexamined.

Another argument for the palaeognathous palate being primitive within birds is the suggestion that it is present in the theropod dinosaurs (Gingerich 1976: 31). To be sure, the reconstruction of the palate of *Tyrannosaurus* by Osborn (1912) shows some resemblances to that of the palaeognaths, but (1) *Tyrannosaurus* lacks the basic organization of the avian (and palaeognath) skull—there is, for example, no basisphenoid rostrum—and (2) *Tyrannosaurus* is on a specialized side-line of theropod phylogeny and is only distantly related to those groups thought to be close to *Archaeopteryx* and birds (Ostrom 1976, Tarsitano and Hecht 1980). Finally, the skull of *Deinonychus,* another theropod dinosaur said by Gingerich (1976: 31) to have a palaeognathous palate, is so poorly preserved (Ostrom 1969) that such a conclusion cannot be made given the available material.

A second line of reasoning sometimes used to argue against palaeognath monophyly is that their palate and open ilioischiatic fenestra are neotenic and therefore could have arisen independently a number of times (e.g. Feduccia 1980: 133; see also de Beer 1956). Without belaboring the point, I merely note that an argument of neoteny is a *prima facie* admission that the similarities in question are derived and not primitive, that is, the adult condition of the ancestor is "replaced" in the descendant by the juvenile condition (Nelson 1978, Eldredge and Cracraft 1980). It also might be noted that there is no strong evidence to suggest that nonpalaeognathous birds actually have a palaeognathous palate (as defined above and in Bock 1963) in their early development.

The open ilioischiatic fenestra may well be primitive, for *Archaeopteryx* certainly possessed one (although even here, despite the varying interpretations of the pelvis of *Archaeopteryx,* the latter genus and the palaeognaths were very different from one another). *Hesperornis* and *Ichythyornis* also had an open fenestra. Because of the phylogenetic conclusions discussed earlier (Division 1; and also Cracraft in press), however, the condition in *Hesperornis* is probably a secondarily derived character, and the same may be true for *Ichthyornis* if the latter is related to the charadriiforms, as seems likely. If palaeognaths are neotenous as many claim, then the open ilioischiatic fenestra can be viewed as a valid derived character.

The relationships of the palaeognath taxa expressed in this classification follow my earlier analysis (1974b). There has been recent biochemical work that argues for a different set of relationships (Sibley and Ahlquist 1980, 1981; Prager et al. 1976). These data, and the methods used to analyse them, will be the subject of a

separate paper. Rich (1979, 1980) has undertaken an extensive reanalysis of the postcranial morphology of palaeognaths and her conclusions do not differ from mine in any significant way.

These birds are traditionally placed in six or seven orders; this classification recognizes one. The palaeognaths are placed in a separate division, because at this time there is no indication of their close relatives within birds. I reiterate my opinion (and that of Bock 1963, and others) that palaeognaths are not the primitive sister-group of birds, although they are an ancient assemblage. The discovery of their sister-group remains an important systematic problem.

DIVISION 3: ORDERS CICONIIFORMES, FALCONIFORMES

The placement of such disparate orders in the same Division may seem unwarranted, and, admittedly, there is no clear evidence for this. Likewise, there is no strong evidence for placing either close to any other nonpasseriforms (see remarks below). There are general similarities in the skeletons of the relatively more primitive member of each order (e.g. ardeids, cathartids). If Wetmore's reconstruction (1944) of the long-legged vulture, *Eocathartes grallator,* is correct, then perhaps this form suggests falconiforms had long-legged ancestors. The view that the two orders may have a relationship is not new (Fürbringer 1888, Ligon 1967). Their placement in Division 3 is tentative and boldly hypothetical.

The systematic positions of the taxa assigned to the order Ciconiiformes have engendered considerable controversy. Many authorities have thought them to be closely related, but probably as many others have disputed this view. In this century the notion of monophyly has been the more common interpretation; nevertheless, strong evidence for this has never been presented. Recently, some alternative phylogenetic hypotheses have been proposed, focusing primarily on the systematic position of the flamingos (Phoenicopteridae). In a series of papers Feduccia (1976, 1977a, 1978) argued that flamingos are related to charadriiforms; Olson (1979) suggested that ibises (Threskiornithidae) represent a "transitional group" between charadriiforms and gruiforms, that the Shoebill (Balaenicipitidae), Hammerhead (Scopidae), and storks (Ciconiidae) may be related to pelecaniforms, and that herons (Ardeidae) are primitive gruiforms; and, finally, Olson and Feduccia (1980a) proposed that flamingos are related to recurvirostrid charadriiforms.

Arguments against the monophyly of ciconiiforms generally have two components. First, it is noted how different the taxa are from one another; this has been the predominant mode of reasoning. Second, systematists may propose alternative relationships, thereby implying that the ciconiiform taxa do not constitute a monophyletic group. The studies cited above use both these components. The first can be rejected, because differences alone are insufficient grounds to conclude nonrelationship (see discussion of Division 4). Hypotheses about alternative relationships, on the other hand, do stand as direct arguments against ciconiiform monophyly. At this time only two alternative hypotheses—that flamingos are related to recurvirostrids and that *Balaeniceps* is a pelecaniform—have been supported by any critical evidence.

My interpretation of the available systematic data and the structure of the arguments about the phylogenetic position of flamingos and *Balaeniceps* reinforces the traditional opinion that ciconiiforms probably are a related assemblage of birds. It

is not possible to analyze in any detail in this paper the extensive data presented by Olson and Feduccia (1980a), but it is possible, I think, to cast considerable doubt on the hypothesis of a flamingo-recurvirostrid relationship. At the same time, one can note some of the data that are consistent with ciconiiform monophyly. A more complete evaluation of ciconiiform inter-relationships is in preparation.

In his earlier papers Feduccia (particularly 1976) postulated a relationship between flamingos and recurvirostrids because of (1) similarities between an Eocene fossil, *Presbyornis pervetus,* and both flamingos and recurvirostrids, and (2) similarities between flamingos and recurvirostrids in characters of the tarsometatarsus and proximal end of the humerus; the available skull fragments of *Presbyornis* were interpreted to be similar to flamingos and ducks and not like shorebirds. On the basis of this evidence Feduccia (1976: 600) postulated that charadriiforms are the sister-group of flamingos and ducks, with *Presbyornis* being a basal member of the latter lineage. In his next paper Feduccia suggested that an ancestral shorebird stock gave rise to *Presbyornis,* which could have been similar to a prototype of the ancestor that gave rise to ducks on the one hand and flamingos on the other (Feduccia 1977a: 720). The following year, without any new evidence being presented, Feduccia (1978: 301) hypothesized that an ancestral shorebird stock gave rise to flamingos on the one hand and to *Presbyornis* on the other; it was a *Presbyornis*-like ancestor that gave rise to ducks. In these latter two papers similarities (or relationships) of *Presbyornis* or flamingos to recurvirostrids are either not mentioned or not stressed. Finally, Olson and Feduccia (1980a) postulate that flamingos have a relationship with recurvirostrids and that *Presbyornis* is instead genealogically closer to anseriforms (Olson and Feduccia 1980b; see discussion of Division 4).

With *Presbyornis* now eliminated from the discussion of a flamingo-recurvirostrid relationship Olson and Feduccia (1980a) support their hypothesis with two lines of argumentation: (1) flamingos are exceeingly similar to the Australian Banded Stilt (*Cladorhynchus leucocephalus*) in life history and anatomy and different from ciconiiforms, and (2) a new fossil flamingo, *Juncitarsus gracillimus,* from the Eocene of North America is intermediate between recurvirostrids and flamingos.

Olson and Feduccia (1980a) demonstrate some remarkable similarities between *Cladorhynchus* and flamingos, but they seem to be uncertain how to interpret these; their most specific hypothesis is that "flamingos evolved directly from the Recurvirostridae rather than from a proto-recurvirostrid" (p. 67). But what, exactly, does this mean? It might suggest that flamingos are the sister-group of *Cladorhynchus,* and these two the sister-group of *Recurvirostra* plus *Himantopus*; indeed, the logical structure of their presentation essentially compels them (p. 67) to make this conclusion (it is claimed, after all, that flamingos and *Cladorhynchus* share many derived characters). Furthermore, they suggest (p. 21) that *Cladorhynchus* is "intermediate" between the Recurvirostridae (apparently *Recurvirostra* and *Himantopus*) and flamingos. The only other cladistic argument that might make sense in light of their data would be that flamingos are the sister-group of recurvirostrids, but they reject this alternative (p. 67).

I believe that the similarities between flamingos and *Cladorhynchus* will eventually be interpreted as convergences. An hypothesis of relationship between flamingos and *Cladorhynchus* has not been placed within the context of a phylogenetic analysis of the charadriiforms. Olson and Feduccia (1980a) claim repeatedly that flamingos are charadriiforms and within the suborder Charadrii, but they never

present the relevant evidence. We need to know what the derived characters are that define the hierarchical levels within the charadriiforms, and we need to place flamingos within those groups on the basis of shared characters. Second, flamingos are not shown to belong to the Recurvirostridae. In their discussions of the anatomical evidence, the characters of *Recurvirostra* and *Himantopus* are conspicuously absent; therefore, we do not know to what degree the characters purported to be derived similarities of *Cladorhynchus* and flamingos are more general recurvirostrid or chardriiform characters. A critical question is what are the similarities among flamingos, *Cladorhynchus, Recurvirostra,* and *Himantopus* that define them as a monophyletic group within the Charadrii? Third, Olson and Feduccia (1980a) attempt to buttress their hypothesis by repeated references to the differences between flamingos and ciconiiforms (particularly ciconiids). But, is it not possible for two groups to be closely related cladistically and yet be different? Moreover, by over-emphasizing differences, Olson and Feduccia naturally chose not to see the possibilities of similarities among flamingos and ciconiiforms. Fourth, I suspect that the fossil *Juncitarsus* is not related to flamingos (at least the tarsometatarsal elements do not appear to be phoenicopterid), but probably is a charadriiform. The hypotarsus is totally unlike all known phoenicopterid genera, both fossil and Recent, in having two deep tendinal canals (the fossil does not have the derived characters of the hypotarsus that define it as a flamingo; see below). It may be that the humeri, not in direct association with the tarsometatarsi, are representatives of a fossil flamingo, but this needs further study. In any case, the argument that *Juncitarsus* is a phyletic intermediate between flamingos and recurvirostrids is not supported by the evidence (it is also a peculiar claim, logically speaking, unless *Juncitarsus* is shown to be an "intermediate" between *Cladorhynchus* and flamingos, which is the only relevent hypothesis consistent with the other data and arguments presented by Olson and Feduccia).

My preliminary studies suggest that there are two moderately well-defined lineages within the Ciconiiformes, one comprising flamingos, storks, and ibises, and the other herons and *Balaeniceps*. Evidence that these two lineages are sister-groups is more circumstantial. In terms of pure phenetic resemblance they all have very similar humeri, pelves, and sterna. They all apparently have the iliotrochantericus medius muscle poorly separated (or not at all) from the iliotrochantericus anterior (Vanden Berge 1970: 329). Also, the Hammerhead (*Scopus*), although appearing to share derived characters with the first lineage, shares some characters with ardeids and *Balaeniceps* that might be interpreted as being derived at a higher hierarchical level; this "intermediacy" of *Scopus* suggests a sister-group relationship between the two lineages.

Ciconiids, phoenicopterids, and threskionithids share a hypotarsus that has lost hypotarsal canals and instead has two well-developed hypotarsal ridges (and a single, deep groove), a deep intercondylar fossa of the tibiotarsus, four heads to the gastrocnemius, the two heads of the pubo-ischio-femoralis (adductor longus et brevis) either narrowly separated or not separated (not widely separated as in ardeids and *Balaeniceps*), and the medial condyle of the quadrate aligned more or less perpendicular to the long axis of the pterygoid. *Scopus* is similar in some of these characters.

Storks and flamingos share further derived conditions of the hypotarsus and distal tibiotarsus. They also have exceedingly similar otic and basitemporal regions of the skull (which are, by the way, not similar to the typical charadriiform condition

possessed by recurvirostrids). Both lack the peroneus brevis, a derived condition. The iliacus of storks and phoenicopterids is "short and stout" (Vanden Berge 1970: 331), not long and narrow; the former condition is probably derived. Furthermore, immunological distance data are not inconsistent with a stork-flamingo relationship (A. H. Brush pers. comm.), and apparently neither are DNA distance data (see comments in Parkes 1978: 9).

The ardeids and *Balaeniceps* are probably sister-groups within the ciconiiforms. They show a number of similarities in the skeleton—particularly in the distal tibiotarsus, tarsometatarsus, proximal humerus, pelvis, and quadrate—but, until we have a better estimate of the close relatives of the ciconiiforms, it will be difficult to determine the polarity of these characters. Both have lost the ambiens and both have the insertion of iliofemoralis externus (gluteus medius et minimus) posterior to that of the ischiofemoralis (Vanden Berge 1970); these are apparently derived conditions.

Balaeniceps has been hypothesized to be related to pelecaniforms (Cottam 1957, Olson 1979). I believe the similarities noted by these authors are convergences. As I will detail elsewhere, *Balaeniceps* cannot be interpolated into a phylogeny of the pelecaniforms (see Division 1), that is, it does not possess the defining characters of each hierarchical level within the phylogeny, and the similarities with pelecaniforms all seem to be correlated with the unique methods *Balaeniceps* has for capturing a main food resource, lungfish (i.e. the Shoebill crashes into dense mats of vegetation much like pelecaniforms crash into water; this may explain the fusion of the furcula and sternum).

The important point of this brief discussion is that despite the obvious differences among the various ciconiiform taxa, there are characters, shared hierarchically, that are consistent with ciconiiform monophyly. Clearly, much more work needs to be done, but, because alternative hypotheses are not as yet convincing, I follow a more traditional approach and unite the families in a single order.

The morphology and interrelationships of the Falconiformes have been debated incessantly. Moreover, the possible relationship between falconiforms and owls (Strigidae) has produced a large literature. Recently, Jollie (1976–1977) catalogued the morphological differences among the falconiform taxa and concluded that the order is polyphyletic; Olson (1979: 168), basing his opinion on Jollie's work, has called the Falconiformes "a totally artificial assemblage." For reasons already noted above (also see Division 4) differences do not signify nonrelationship, and no one to my knowledge has provided any satisfactory evidence that specific falconiform families are related to other groups of nonpasserines.

My ongoing studies suggest the falconiforms are a monophyletic group, although this hypothesis needs much more evaluation. Moreover, it is apparent that many 19th century avian morphologists and systematists were correct in assigning strigids to this order; the similarities between some falconiforms and owls are interpretable not as convergences but as shared derived characters.

Admittedly, a strong case for falconiform monophyly has not yet been presented. They can be characterized by a raptorial bill; the pelves are similar in having a large, round, ilioischiatic fenestra, a very deep ilioischiatic plate, and strongly curved pubes. They also exhibit similarities in the furculum and sternum. Because of these general similarities, and, as there are no satisfactory opposing hypotheses, it is best to maintain the order.

The Secretary Bird (Sagittariidae) is so highly derived in much of its morphology that systematists have had difficulties with its relationships. But the skull is so similar to other falconiforms, and at the same time does not indicate relationships elsewhere, that its placement in this order seems correct (there is no evidence, for example, for a relationship to the cariamids as is sometimes suggested; see Division 5). The Secretary Bird retains the primitive condition of the feet and other aspects of its anatomy (e.g. pelvis) compared to the taxa in the infraorder Falconi.

Owls can be included in the Falconi, because they possess a derived tarsometatarsal and pelvic morphology shared with pandionids and accipitrids (including falcons); the Falconi (including owls) also have a unique pelvic myological pattern in that they have lost the piriformis pars iliofemoralis, the flexor cruris lateralis (semitendinosus) and accessory semitendinosus, and the viniculum connecting the flexors of digit III. Strigids also possess the derived characters of higher hierarchical levels (order, suborder). I have been unable to find evidence for a relationship between owls and any other group of nonpasserines. Caprimulgiforms are most often mentioned, but the morphological organization of caprimulgiforms is clearly similar to apodiforms and not strigids (see Division 8). What is not often realized by contemporary ornithologists is that numerous 19th century workers saw the many similarities of hawks and owls as evidence of close relationship; it was 20th century systematists who overemphasized differences and concluded convergence. Accipitrids and pandionids have lost the basipterygoid processes, whereas strigids retain the primitive condition.

DIVISION 4: ORDERS ANSERIFORMES, GALLIFORMES

The taxa included in this division present a number of controversial problems in avian systematics. First is the question of whether these two orders should be associated with one another. A new perspective on this issue has been introduced by Olson and Feduccia (1980b), who claim that anseriforms are derived from charadriiforms. The primary basis for this conclusion is an Eocene fossil, *Presbyornis pervetus,* which is interpreted to have the head of a duck and the postcranial skeleton of a shorebird; at the same time Olson and Feduccia argue that there is no positive evidence to support a relationship between anseriforms and galliforms.

Space does not permit a thorough examination and critique of the paper by Olson and Feduccia, but I will summarize some of my main reservations. First, no specific phylogenetic hypotheses are proposed. Presumably, *Presbyornis* would have to be considered more closely related to anseriforms than to charadriiforms (because the anatid-like skull is clearly derived), but without specific reasons they place *Presbyornis* in its own family within the Charadriiformes. Nor is it hypothesized to which group of charadriiforms (if not the entire order) *Presbyornis* (+anseriforms?) is most closely related. In earlier papers Feduccia (1976, 1978; Feduccia and McGrew 1974) variously interpreted the postcranial morphology to be similar to recurvirostrids or to flamingos (see discussion of Division 3), but Olson and Feduccia (1980b: 12) now indicate those similarities to flamingos are actually primitive charadriiform characters (Feduccia, in his earlier papers, implied the characters were derived; Olson and Feduccia do not mention which characters they have in mind or why they are now considered primitive). Second, as the above remarks should make evident, Olson and Feduccia do not attempt to define monophyletic groups

on the basis of derived characters. It is not stated in their paper exactly which characters link *Presbyornis* and anseriforms to all or part of the charadriiforms. Third, they adopt an approach to paleontological interpretation that frequently leads to erroneous conclusions (Cracraft 1980): the morphology of fossils is essentially considered *ipso facto* to be primitive, and the morphology and phylogenetic relationships of the fossil taxon are not interpreted within the context of hypotheses of relationship for the Recent taxa purported to be united by the fossil. Thus, no discussion of charadriiform relationships is presented, and that for anseriforms takes a curious slant: they claim the anhimids are highly derived relative to anseriforms (no evidence is presented for this) and that (p. 22) *Anseranas* is actually more primitive than the anhimids. Such a conclusion would necessitate either (1) the evolution of the anatid cranial and postcranial organization twice, or (2) the derivation of anhimids from an ancestor that had an anatid level of organization. I find both conclusions less parsimonious than accepting *Anseranas* to be more closely related to other anatids than either is to anhimids. Fourth, they dismiss a galliform-anseriform relationship by claiming the two groups are different, but differences in themselves do not constitute a valid argument for rejecting a hypothesis of relationship (they do, in this case, offer an alternative: that anseriforms are related to charadriiforms). The point is that the differences between anseriforms and galliforms may simply be defining the two groups as separate lineages, and therefore those differences would be totally irrelevant with respect to testing a hypothesis of relationship of these two taxa relative to a third. It is an elementary problem of phylogenetic reasoning: only similarities test phylogenetic hypotheses, and one must undertake a character analysis (i.e. postulate primitive-derived sequences) in order to have a basis for that test.

Given the above reasons, I do not believe a case has been made for a relationship between anseriforms and charadriiforms. Certainly one must keep an open mind regarding the relationship between anseriforms and galliforms, for I agree with Olson and Feduccia that such a relationship is not well documented. Nevertheless, there is some tentative evidence to warrant keeping them close to one another. Prager and Wilson (1976, 1981) have suggested a close relationship based on immunological distances of various proteins. For two proteins, transferrin and albumin, anseriforms and galliforms clustered next to one another and were distant from other groups including the charadriiforms (but based only on samples from two species of gulls). Anseriforms and galliforms also apparently have detailed similarities in their stereotypic display behavior not shared with other birds (K. Lorenz, pers. comm.). Both anseriforms and galliforms have a malate dehydrogenase mobility of 100 (Kitto and Wilson 1966). Given the mobility distribution of this enzyme within the class Aves, a mobility of 100 is very likely to be primitive. As such, this similarity is not to be considered evidence of close relationship, but I call attention to it because the entire order Charadriiformes apparently has a derived mobility of 55. If anseriforms were derived from within the order charadriiforms, as the published interpretations of the postcranial morphology of *Presbyornis* might suggest (Feduccia 1976, 1978; Olson and Feduccia 1980b), then it is surprising that anseriforms show the primitive condition. Galliforms (except apparently *Opisthocomus*) and anseriforms share an entepicondyloulnaris muscle, which is apparently found only in them and the tinamous and kiwis (George and Berger 1966, Zusi and Bentz 1978). If this distribution is correct, then several interpretations might be indicated:

(1) the muscle could have arisen independently in all four groups, (2) anseriforms and galliforms could be related to palaeognaths (with the muscle being lost in higher ratites), or (3) the muscle could have arisen independently in palaeognaths and in a galliform-anseriform lineage. Preference for one of these hypotheses depends on the concordance of each with other derived characters. The second and third alternatives are more parsimonious than the first, and in either case the evidence is consistent with a galliform-anseriform relationship. Finally, some similarities in the skulls can be suggested: the basicrania are similar in being inflated and with the exits for the cranial nerves being in similar topographical positions; the basipterygoid processes are similar in being relatively large, oblong, set somewhat anteriorly on the basisphenoid rostrum, and being relatively close to one another and not greatly separated by a wide rostrum; and the articulating surfaces of the quadrate articulations are similar in shape and position.

In summary, then, I tentatively include galliforms and anseriforms in the same division. Obviously, the problem needs much further study, and I agree the evidence for such a relationship is not strong as yet. But I find it disquieting for theoretical reasons (Cracraft 1980), when two higher taxa (anseriforms, charadriiforms) are placed together because a fossil is said to have a head only similar to one taxon and a postcranial skeleton only similar to the other taxon. The evidence of comparative morphology and systematics suggests that mosaic evolution does not work as absolutely as this, and we should require stronger evidence for postulating such a relationship, particularly in two groups that do not appear to share any derived characters. This is the crux of the argument: what are the synapomorphies uniting anseriforms and charadriiforms? The morphology of *Presbyornis* is silent on this question.

The second major systematic problem presented by the taxa in this division is the phylogenetic relationships of the Hoatzin (Opisthocomidae), which has been viewed as being morphologically aberrant by all who have investigated its relationships. Usually placed with the galliforms, Sibley and Ahlquist (1973) have argued that *Opisthocomus* "without qualification" belongs in the subfamily Crotophaginae of the Cuculidae. They based their conclusion on data provided by acrylamide gel electrophoresis of egg-white proteins.

There seems little doubt that the electrophoretic patterns published by Sibley and Ahlquist (1973) suggest similarities between *Opisthocomus* and *Guira* and *Crotophaga,* but, using comparable techniques, Brush (1979) found no clear-cut similarities between *Opisthocomus* and cuckoos; indeed, employing different buffers gave strikingly different electrophoretic patterns, thus yielding an ambiguous systematic interpretation. *Opisthocomus* might be related to cuckoos, but I find very little evidence to support it. The osteology of *Opisthocomus* is much more like galliforms than cuculiforms (pers. obs.), not only in terms of cranial anatomy but postcranial as well. Immunological distance data on ovalbumins indicate *Opisthocomus* is closer to galliforms than to cuculiforms (Brush 1979). The systematic position of *Opisthocomus* needs further analysis, and until that time I tentatively retain the family in the Galliformes.

Morphologically, the megapodes are clearly the sister-group of the other galliforms. The Phasiani are united by having, among other things, a greatly reduced (or lost) ectethmoid bone, a long, thin orbital process of the quadrate, and a basitemporal plate that became increasingly enlarged and bulbous. Within the Phasiani,

the taxa of the superfamily Phasianoidea share some derived characters not possessed by the Cracidae, including a sternum with long, thin posterolateral processes. Cracids appear to be very divergent genetically, as assayed by immunological techniques (Prager and Wilson 1976). Within the Phasianidae, the guinea-fowls (Numidinae) appear to be the sister-group of the pheasants, grouse, turkeys, and New World quail. A phylogenetic analysis of the Phasianinae is an urgent problem.

DIVISION 5: ORDERS GRUIFORMES, CHARADRIIFORMES, COLUMBIFORMES

These three orders have often been associated, but their interrelationships have not yet been resolved satisfactorily. There is reason to maintain this association (see below), first, for no other reason than it stands as a working hypothesis, and, second, because no alternative hypothesis of interordinal relationships seems better.

The order Gruiformes is much more cohesive than many previous authors have believed, and several well-corroborated hypotheses can be proposed (Cracraft 1973, MS). The relationships of three families, in particular, remain uncertain. The Mesitornithidae of Madagascar may represent an early lineage of gruiforms, because they possess three characters that are apparently primitive within the order: schizorhinal nostrils, large ectethmoid, and deep sternal notches. The Turnicidae are also primitive, and, *if* they can be shown to be cladistically related to other gruiforms, then some of their more primitive characters might serve to unite them (at a higher hierarchical level where the characters would be derived) with the columbiforms (e.g. Lowe 1923). Finally, the relationships of the Otididae are also perplexing. They cannot be placed easily within the Grues (Cracraft MS) nor near the cariamids, as has been suggested by some authors. Although they are very likely to be more closely related to gruiforms than any other group, their exact relationships, relative to the Grues and Ralli, remain unresolved.

The phylogenetic relationships of the suborder Grues have been documented elsewhere (Cracraft 1973, MS). The inter-relationships of these families have repeatedly confused systematists for over a century, because these workers emphasized differences rather than similarities and often attempted to unite groups on the basis of primitive characters. Using postulated derived characters, it is possible to define each of the lineages. Many of these families—psophiids, cariamids, rhynochetids, eurypygids—are frequently characterized as "ancient" or "relict" families whose interrelationships remain obscure. Actually, it is possible to define a monophyletic group, the Psophii, for all four families, and, if their history is interpreted within the framework of more general Southern Hemisphere biogeographic patterns exhibited by plant and animal taxa, then these groups are seen to be members of biotas that were fragmented by continental drift or by intra-continental vicariance events (Cracraft MS); they are not interpretable as strict relicts. It can be noted here that the phororhacoids, which underwent a remarkable radiation of flightless, predatory forms in South America, have their closest relationship to the cariamids.

The heliornithids and rallids show similarities in their skeletons, particularly in their skull morphology (pers. obs.). Therefore, I unite them as a preliminary hypothesis that is clearly in need of further evaluation.

Few orders have invited so much systematic attention as the Charadriiformes, and a number of workers have recently added to the large literature developed by

19th and early 20th century ornithologists (e.g. Jehl 1968, Zusi and Jehl 1970, Fjeldsa 1976, Strauch 1978, Stegmann 1978). Considerable disagreement, not only with respect to methods but also with results, exists among these workers (see, for example, Mickevich and Parenti 1980). Because of this, and primarily because I have only initiated preliminary studies of my own, the classification proposed here should be considered highly tentative; it does, I believe, represent our current knowledge of relationships better than previous classifications.

One of the suborders recognized here, the Alcae, is clearly monophyletic; the other two are probably paraphyletic, but at present no corroborated hypothesis of their interrelationships has emerged.

The relationships of the alcids have confounded all workers, primarily because they have diverged markedly in most characters used in traditional studies, and this highly apomorphous condition has obscured the search for similarities with other charadriiforms. It is not necessarily the case, therefore, that alcids should be viewed as a basal lineage of the charadriiforms, as generally has been done.

The suborder Charadriomorpha includes five infraorders, several of which are placed here only provisionally.

The relationships of the Dromadidae (crabplovers) seem to be with the assemblage of taxa included in the Charadriomorpha rather than to the Scolopaci (Jehl 1968, Fjeldsa 1976, Strauch 1978), but a more specific hypothesis has not yet been well corroborated.

The Lari also are apparently related to the Charadriomorpha rather than the Scolopaci (Fjeldsa 1976, Strauch 1978). Using character-compatibility analysis, Strauch (1978) placed stercorariids close to larids, with sternids being more primitive than either and with rhynchopids being more divergent and on a side branch (the methods did not yield an unambiguous branching sequence). Mickevich and Parenti (1980) reinterpreted Strauch's analysis and produced a cladogram with no sister-group relationships among these four taxa (i.e. the cladogram had four branches from the same node). My studies suggest that gulls and terns are sister-taxa (in this classification, united as the Laridae) and that they are most closely related to rhynchopids. These three taxa share derived characters of the humerus, tarsometatarsus, and skull. Stercorariids, on the other hand, are more primitive in their morphology.

The sheathbills (Chionididae) comprise another group whose relationships have been uncertain. Yudin (1965) and Jehl (1968) placed chionidids and thinocorids in the same superfamily close to the Scolopaci; Fjeldsa (1976) adopted a similar view. Other morphological studies suggest similarities between chionidids and various charadriomorph taxa (Burton 1974, Strauch 1978, pers. obs.). I tentatively follow this latter view. I also include the Magellanic Plover (*Pluvianellus socialis*) in the Chionididae rather than recognizing yet another monotypic family. *Pluvianellus* shares some apparent derived characters with *Chionis* (Strauch 1978) and also is similar behaviorally (Jehl 1975). The relationships of the Thinocoridae to the Chionididae are still a matter of doubt. Strauch (1978) considered thinocorids to be related to the Scolopaci. Stegmann (1978) drew attention to the general similarity in wing anatomy between thinocorids and chionidids. Currently available data are clearly ambiguous, and I place thinocorids close to chionidids simply as a working hypothesis (see Sibley et al. 1968, for a summary of previous opinion).

The Burhinidae variously have been thought related to the Scolopaci, charadriomorph taxa, and even to the gruiforms. My own preliminary observations suggest

burhinids share characters, probably derived, with various charadriomorph taxa. Accordingly, I tentatively assign the burhinids to the Charadriomorpha (see also Jehl 1968).

Of the families placed in the infraorder Charadrii, only the Glareolidae might be removed by some workers. I follow Jehl (1968) and Strauch (1978) and include glareolids within the Charadrioidea, and these workers have also presented evidence for a close relationship of the Haematopodidae and Recurvirostridae.

I follow Jehl (1968) in placing the Painted Snipe (Rostratulidae) close to the Jacanidae. Not only are the two groups similar in plumage patterns of the young, but their egg-white protein patterns are said to be unique within charadriiforms (Sibley and Ahlquist 1972), and they share some skeletal similarities in the skull, tarsometatarsus, and pelvis (pers. obs.).

It has now become generally accepted that the "Scolopacidae" of earlier classifications (e.g. Wetmore 1960) is an unnatural group in that phalaropes (generally placed in a separate family) may be related to a portion of the "scolopacids" and that other "scolopacids" may be more closely related to the Jacanoidea. Accordingly, until future work unravels these relationships, I recognize one family, the Scolopacidae, in the sense of Jehl (1968). Present evidence indicates that this taxon constitutes a monophyletic assemblage within the charadriiforms.

In recent years some authors have reinvestigated the old idea that sandgrouse (Pteroclidae) form a link between pigeons (Columbidae) and charadriiforms (MacLean 1967, 1969; Stegmann 1969, 1978; Fjeldsa 1976). A cladistic interpretation of the available evidence suggests that pteroclids are the sister-group of columbids. The charadriiform characters of sandgrouse and pigeons can be interpreted to mean either (1) that the columbiforms are the sister-group of the charadriiforms or (2) that they are the sister-group of a portion of the charadriiforms (Fjeldsa 1976, for example, has identified the Glareolidae). In my opinion these alternatives (and possibly others, as the gruiforms frequently have been allied to charadriiforms) have not yet received a satisfactory evaluation.

I include the Dodo (*Raphus*) and Solitaire (*Pezophaps*) in the Columbidae. To place them in their own family within a phylogenetic classification would imply a sister-group relationship to the columbids. The systematic problem here is to identify their close relatives within the columbids.

DIVISION 6: ORDER PSITTACIFORMES

The parrots (Psittacidae) are so morphologically distinct from other birds that their relationships to other groups have remained unresolved. The two groups perhaps most often considered to be close relatives are the pigeons and cuckoos (see summary in Sibley and Ahlquist 1972), but evidence is meager at this time. Because the placement of the parrots within other nonpasserines would be little more than speculation, the Psittacidae are relegated to their own division.

DIVISION 7: ORDER CUCULIFORMES

The cuckoos (Cuculidae), like the parrots, are highly apomorphic morphologically. There is reasonably strong evidence for accepting a sister-group relationship between the turacos (Musophagidae) and cuculids, but the affinities of both families to other

birds remain uncertain. For reasons already discussed, I exclude *Opisthocomus* from the Cuculiformes (see Division 4).

DIVISION 8: ORDERS CAPRIMULGIFORMES, APODIFORMES

For many years these two orders have presented a number of interesting systematic questions. For example, the question has been asked repeatedly whether the caprimulgiforms are more closely related to owls or to apodiforms, and whether swifts and hummingbirds are actually closely related instead of merely possessing convergent similarities. Several ongoing studies provide evidence to answer these questions. I noted earlier my reasons for assigning owls to the Falconiformes. Another study indicates that caprimulgiforms and apodiforms are each other's closest relative (Cracraft MS). The two groups are defined as forming a monophyletic lineage by many derived characters, particularly in the skull. Some of these characters include a very short, broad bill with the nasal process of the premaxilla very thin and curved; the external nares very large and extending much the length of the bill; the jugal bars very long, thin, and joined to the premaxilla at the far anterior end of the skull (because of a fore-shortened bill); and the orbital process of the quadrate greatly reduced. Some of these characters have been secondarily modified in several families, especially the podargids, steatornithids, and trochilids.

Within the caprimulgiforms it frequently has been held that the steatornithids are so different as to be rather distantly related to the other four families (although virtually all workers have agreed on the monophyly of the order). My investigations indicate this may be mistaken. There are two well-defined lineages: aegothelids and podargids on the one hand, and caprimulgids and nyctibiids on the other. At this time the evidence suggests *Steatornis* is more closely related to the latter group. Thus, *Steatornis,* caprimulgids, and nyctibiids share basipterygoid processes, a humerus with the impression of brachialis anticus very well marked and with a thin external condyle (this may be primitive but can be interpreted as being derived independently of the apodiforms), and a sternum that has a single, short, blunt posterior lateral process.

The caprimulgids and nyctibiids share many skull characters, including a peculiar quadrate (e.g. condylar structure, apparent complete loss of orbital process) and a reduction in the length of the dentary relative to the post-dentary bones. Likewise, the aegothelids and podargids share derived characters, including a double-notched sternum with long posterior processes, the anterior iliac blades extremely well developed, and a peculiar egg-white protein pattern (Sibley and Ahlquist 1972: 196, Fig. 33).

The osteology of swifts and hummingbirds offers strong support for a sister-group relationship (Cracraft MS). This is especially true of the cranial characters, for which one would be hard pressed to construct an argument of convergence, as has been done for some of the postcranial similarities because of presumed similarities in locomotor habits (which are actually quite different). Some of these characters include a peculiar quadrate-squamosal articulation in which the zygomatic process abuts against the lateral and anterior surfaces of the quadrate; a quadrate in which the dorsoposterior surface is excavated and pneumatic (one or more foramina present); interpalatine processes elongated; a very distinct humerus with the olecranal fossa extremely deep, a deep groove between the external condyle and ectepicon-

dyle, the development of a process proximal to the ectepicondylar prominence and located near the middle of the shaft, to name a few; a sternum squared posteriorly with no notches (and thus no processes); and a cruciform origin of M. splenius capitis (Burton 1971). Swifts and hummingbirds also have a unique form within birds of the enzyme malate dehydrogenase (Kitto and Wilson 1966).

DIVISION 9: ORDERS PICIFORMES, COLIIFORMES, CORACIIFORMES, PASSERIFORMES

This division includes the "higher" nonpasserine orders and the Passeriformes; it has been a general assumption of nearly all modern avian systematists that these taxa constitute a related assemblage, but a precise hypothesis of their interrelationships has not been supported. The idea that passeriforms have a close relationship to the Piciformes probably took hold with the work of Fürbringer (1888), and most recent classifications list the two orders next to each other. This hypothesis is in need of much additional evaluation. As an alternative, it may be that passeriforms are the sister-group either of the Coraciiformes (if that group is monophyletic) or only of a portion of the coraciiforms (some recent studies have almost implied as much; see below). For example, Lowe (1946) listed similarities shared by Piciformes and passeriforms, but he also was including the Upupidae with his piciform taxa. It is certain that upupids are not piciform (as defined below), but rather close to other coraciiforms; however, upupids have a tarsometatarsal and sternal morphology that is the closest counterpart to that of passeriforms to be found within the higher nonpasserines. Whether this is significant with respect to the origin of the Passeriformes warrants further investigation.

The arrangement of the Piciformes presented here is based on a highly corroborated hypothesis of relationships. Undertaking independent cladistic analyses, Swierczewski and Raikow (1981) investigated myological data and Simpson and Cracraft (1981) osteological data, and both studies came to the same phylogenetic conclusions. This classification differs from that of Wetmore (1960) in recognizing three taxa, the Galbulae, Pici, and Capitonoidea, whose contents vary substantially from taxa of the same name in Wetmore's system.

The systematic position of the colies, Coliidae, remains enigmatic. They seem to be of a Division 9 "grade" of morphological organization, but it is entirely possible their relationships lie elsewhere.

The Coraciiformes have always been viewed as a heterogeneous assemblage. Feduccia (1975a, 1977b) suggested that the passeriforms are diphyletic and that suboscines are related to one group of coraciiforms (the "Alcediniformes"). The view that passeriforms are diphyletic has been abandoned (Feduccia 1979), but a diphyletic origin of the coraciiforms is essentially still supported by Feduccia (1980: 180). Maurer (1977), on the other hand, undertook a cladistic analysis of the myological system and concluded that coraciiforms (*sensu* Wetmore 1960) are monophyletic; these taxa are said to share the loss of the ambiens, the loss of the iliofemoralis externus, and the tendons of flexor hallucis longus and flexor digitorum longus are extensively fused (Gadow's type V arrangement).

In my own preliminary studies of the higher nonpasserines, I have been unable to relate any one coraciiform family to a taxon in some other order; therefore, I tentatively accept the hypothesis of coraciiform monophyly. Maurer (1977) was able to resolve relationships within the coraciiforms using myological characters, but I find

apparent contradictions in some of the osteological evidence. Until this problem can be investigated further, a somewhat conservative, noncommittal approach will be followed here.

I agree with Maurer that there is a lineage (here termed the Alcedini) that includes the Alcedinidae and Meropidae on the one hand and the Momotidae and Todidae on the other. These four taxa have the tendon of flexor hallucis longus excluded from the hallux (Maurer 1977), a derived stapes morphology (Feduccia 1975a), and derived characters in the humerus and tarsometatarsus (pers. obs.). Feduccia (1975a) includes the trogons (Trogonidae) with this assemblage on the basis of an apparently derived stapes morphology, but in trogons flexor hallucis longus supplies the hallux (a primitive condition), and I have been unable to find derived similarities in the skeleton shared between trogons and the other Alcedini. Although I agree that trogons are related to these coraciiforms, the evidence is still equivocal with respect to their exact placement; this is the reason for assigning them to a separate infraorder within the Alcedines. Maurer (1977) relates trogons to meropids and alcedinids, because all have lost the flexor cruris lateralis pars accessorius.

I hypothesize that the Coracii are related to the Alcedini on the basis of sharing a unique lacrimal-ectethmoid complex: the lacrimal is large and expanded medially, and the ectethmoid is a spur of bone that fits into a notch on the lacrimal. This condition has been modified further in the Momotoidea (lacrimal slightly reduced in todies, lost in motmots), and the lacrimal is reduced in the meropids.

In an earlier paper (1971) I included the Cuckoo-roller (Leptosomatidae) in a phylogenetic hypothesis with the true rollers (Coraciidae) and ground-rollers (Brachypteraciidae). That study was insufficiently comparative, and I now have some doubts about the affinities of *Leptosomus;* Maurer (1977) unites the three families (see also Cracraft 1971: 725, for characters that appear to indicate monophyly). *Leptosomus* appears primitive in many respects and does not have the characters of the suborder Alcedines. It is possible, however, that the differences of *Leptosomus* are derived conditions within the Alcedini. Until their relationships can be examined in more detail, I place the Leptosomatidae within the Coracii. In any case, coraciids and brachypteraciids are sister-groups.

The hoopoes and wood-hoopoes are clearly closely related to one another as they share a large number of unique anatomical specializations (see Maurer 1977; pers. obs. of the skeleton). The Upupes may well be the sister-group of the Alcedines as Maurer (1977) indicates; both groups share a fused puboischiofemoralis and have lost the abductor digiti II, and my observations suggest that all share a similar tarsometatarsal structure (modified in todies and motmots).

The hornbills (Bucerotidae) have always been seen as bizarre morphologically, so much so that many earlier workers placed them in their own order. Nevertheless, the bucerotids almost certainly are related to the other coraciiforms (Maurer 1977; pers. obs.) and possibly represent an early lineage. They are placed in their own suborder to signal the uncertainty of their exact relationships within the order.

The order Passeriformes is a large monophyletic assemblage (Raikow 1980, in press) whose interrelationships are very poorly understood (for a survey of the literature see Sibley 1970). Because my own research has focused on the nonpasserines, this section of the classification is based on published accounts of relationships. Through the years a number of passerine classifications have been published, but most of these consist of little more than a linear list of familial-level taxa, and, as

such, phylogenetic relationships are not expressed. The best classification available is that of Mayr and Amadon (1951) in which they attempted to group families according to their presumed relationships. Their classification serves as my starting point, although I have applied a more formal taxonomic structure to their groups. Moreover, I have incorporated the results of subsequent studies. A word of caution is in order, however: I have not made an extensive effort to evaluate these studies with those of my own. Most of them represent the only available hypotheses, and, by following them here, I do not imply the hypothesized relationships are necessarily well corroborated. Many of these studies are based only upon an analysis of the appendicular myology, and their results need verification from other data; in the brief discussion that follows I primarily summarize the conclusions of these studies. It should also be noted that in portions of the passeriform classification, brackets are used to identify hypothesized sister-taxa.

The suboscines (suborder Tyranni) apparently form a monophyletic group based on possession of a derived stapes (Feduccia 1974). The Eurylaimi are often placed in their own suborder, but their relationships are probably with the suboscines (Olson 1971). The relationships of the pittas within the Tyranni are uncertain; thus, I place them in their own suborder. I follow Ames (1970) in separating the Furnarii from what I have termed the Tyrannomorpha. The interrelationships of the families in the Tyrannoidea are still not understood, and it is likely that familial lines will have to be redrawn once generic interrelationships are discerned.

The suborder Passeres is no doubt monophyletic. They have a derived sperm morphology (McFarlane 1963, Henley et al. 1978), derived syrinx, and a derived cranial and tarsometatarsal morphology. The infraorders recognized here generally follow the groupings of Mayr and Amadon (1951). Three families at the beginning of the list have uncertain affinities. The acanthisittids are not suboscines (Feduccia 1975b) and may eventually be shown to be related to some Australasian oscine group. The infraorder Muscicapi contains taxa generally placed next to one another by most workers (e.g. Mayr and Amadon 1951: 36–37). The affinities of the Prunellidae and Motacillidae with other taxa in this infraorder are very uncertain; hence, they are listed as *incertae sedis*. The Muscicapi probably constitutes a paraphyletic group in as much as taxa in other infraorders (e.g. Sitti, Meliphagi) may be related to some of its members. Within the infraorder the Muscicapinae and Turdinae are placed together on the basis of sharing a derived syrinx (Ames 1975). Several studies have suggested relationships among thrushes, dippers, thrashers, and wrens (Morioka 1967, Gulledge 1975), so I place them within the Muscicapoidea; however, it should be noted that these studies were inadequate in terms of methodology or scope of the comparative sample to preclude closer relationship of these families to some of the Sylvioidea. The superfamily Sylvioidea is clearly a problematical taxon given our present knowledge.

The Laniidae of previous workers may be polyphyletic. The bush shrikes are apparently the sister-group of true shrikes, *Pityriasis,* and the prionopids (Raikow et al. 1980). The vangids are included in the infraorder for want of a better alternative.

The taxa of the Bombycilli are also of uncertain relationships. Mayr and Amadon (1951) placed the wood-swallows (Artamidae) in this group, but their affinities are more probably with other Old World groups (see below). I follow the practice of placing *Hypocolius* and *Dulus* with the waxwings and silky-flycatchers, although

evidence for this is not strong, particularly for *Hypocolius*. If silky-flycatchers are related to waxwings, then *Myadestes* is probably best removed from the turdids (Sibley 1973).

Creepers, nuthatches, and titmice are typically placed together but little evidence has been presented. This entire complex warrants more detailed analysis.

The infraorder Meliphagi consists of four Old World nectar-feeding families, and it is their feeding habitats that seem to be the main reason for their close association in most classifications.

The infraorder Corvi has been the subject of recent systematic analyses. Six families, the oriolids, dicrurids, artamids, pycnonotids, irenids, and campephagids are tentatively included, but their association needs further study (see Sibley 1976). There seem to be two monophyletic lineages, but it is still a question whether they are sister-groups (Borecky 1977). Corvids appear to be the sister-group of the grallinids, but, using myological characters, Borecky was unable to corroborate the more traditional linkage between corvids and the ptilonorhynchines-paradisaeinines. Instead, the latter taxa appear closely related to the New Zealand Callaeidae, and that complex is, in turn, related to the starlings (Sturnidae). Borecky (1977) further postulated that the cracticids are the sister-group of the sturnid-callaeid-paradisaeid complex. *Turnagra* is presumably most closely related to the Paradisaeinae. Sibley (1974) has argued that the Menurae are not primitive passeriforms but rather are close to paradisaeids, and other morphological evidence seems to bear out a relationship to the corvine assemblage (M. H. Clench, pers. comm.).

The interrelationships of the taxa included in the Passeromorpha have been studied by Bentz (1979) using myological characters. His phylogenetic hypothesis is followed here although not his classification, which does not express his postulated relationships.

Finally, the nine-primaried oscines (infraorder Fringilli) have been the subject of a cladistic analysis using myological characters (Raikow 1978). Although these data cannot resolve all the branch points, this work suggests some broad relationships. Raikow (1978) was unable to confirm a close relationship between the Vireonidae and the nine-primaried oscines, but until new information about their affinities is presented, it seems best to keep the vireos close to the emberizoids. Not unexpectedly, parulids and thraupids appear to be the basal members of the Emberizoidea. Relationships of some genera previously placed in the Coerebidae are still uncertain. The thraupids are postulated to be the sister-group of what is termed here the Emberizidae. Within the latter the interrelationships are not fully resolved. The cardinalines form one group, the icterids-emberizines another, and the carduelines-drepanidines a third (see also Raikow 1976, 1977a, b). Several of these groups—e.g. emberizines, carduelines—may not be strictly monophyletic (Raikow 1978).

THE CLASSIFICATION

The phylogenetic classification developed above may be summarized as follows:

Class Aves
  Subclass Archaeornithes
              Family Archaeopterygidae
  Subclass Neornithes
    Division 1
      Cohort Gavio-impennes

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        Order Sphenisciformes
                Family Spheniscidae
        Order Gaviiformes
                Family Gaviidae
                        Podicipedidae
    Cohort Stegano-tubinares
    Order Procellariiformes
        Suborder Diomedeae
                Family Diomedeidae
        Suborder Procellariae
                Family Hydrobatidae
                        Procellariidae
    Order Pelecaniformes
        Suborder Phaethontes
                Family Phaethontidae
        Suborder Steganopodes
            Infraorder Fregatae
                Family Fregatidae
            Infraorder Pelecani
                Superfamily Pelecanoidea
                Family Pelecanidae
                Superfamily Suloidea
                Family Sulidae
                        Phalacrocoracidae (inc. *Anhinga*)

Division 2
    Order Palaeognathiformes
        Suborder Tinami
                Family Tinamidae
        Suborder Ratiti
            Infraorder Apteryges
                Family Dinornithidae
                        Apterygidae
            Infraorder Struthiones
                Superfamily Casuarioidea
                Family Casuariidae
                        Dromiceidae
                Superfamily Struthionoidea
                Family Rheidae
                        Struthionidae

Division 3
    Order Ciconiiformes
        Suborder Ardeae
                Family Ardeidae
                        Balaenicipitidae
        Suborder Ciconiae
            Infraorder Scopiae
                Family Scopidae
            Infraorder Ciconii
                Superfamily Threskiornithoidea
                Family Threskiornithidae
                Superfamily Ciconioidea
                Family Ciconiidae
                        Phoenicopteridae

    Order Falconiformes
        Suborder Cathartae
                Family Cathartidae
        Suborder Accipitres
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   Infraorder Sagittarii
    Family Sagittariidae
   Infraorder Falconi
    Superfamily Strigoidea
     Family Strigidae (inc. *Tyto*)
    Superfamily Falconoidea
     Family Pandionidae
     Family Accipitridae
      Subfamily Accipitrinae
         Falconinae

Division 4
 Order Anseriformes
    Family Anhimidae
       Anatidae

 Order Galliformes
  Suborder Opisthocomi
    Family Opisthocomidae
  Suborder Galli
   Infraorder Megapodi
    Family Megapodiidae
   Infraorder Phasiani
    Superfamily Cracoidea
     Family Cracidae
    Superfamily Phasianoidea
     Family Numididae
       Phasianidae

Division 5
 Order Gruiformes
    Family Mesitornithidae, *incertae sedis*
       Otididae, *incertae sedis*
       Turnicidae, *incertae sedis*
  Suborder Grues
  Infrasuborder Grui
    Family Gruidae
  Infrasuborder Arames
   Infraorder Arami
    Family Aramidae
   Infraorder Psophii
    Superfamily Psophioidea
     Family Psophiidae
       Cariamidae
    Superfamily Rhynocheti
     Family Rhynochetidae
      Subfamily Aptornithinae
         Rhynochetinae
     Family Eurypygidae
  Suborder Ralli
    Family Heliornithidae
       Rallidae

 Order Charadriiformes
  Suborder Alcae
    Family Alcidae
  Suborder Charadriomorpha
   Infraorder Dromae
    Family Dromadidae

Infraorder Lari
  Superfamily Stercorarioidea
    Family Stercorariidae
  Superfamily Laroidea
    Family Rhynchopidae
        Laridae
Infraorder Chionae
    Family Chionididae
        Thinocoridae
Infraorder Burhini
    Family Burhinidae
Infraorder Charadrii
  Superfamily Haematopodoidea
    Family Haematopodidae
        Recurvirostridae
  Superfamily Charadrioidea
    Family Glareolidae
        Vanellidae
        Charadriidae
Suborder Scolopaci
  Superfamily Jacanoidea
    Family Jacanidae
        Rostratulidae
  Superfamily Scolopacoidea
    Family Scolopacidae

Order Columbiformes
    Family Pteroclidae
        Columbidae

Division 6
Order Psittaciformes
    Family Psittacidae

Division 7
Order Cuculiformes
    Family Musophagidae
        Cuculidae

Division 8
Order Caprimulgiformes
  Suborder Podargi
    Family Aegothelidae
        Podargidae
  Suborder Caprimulgi
    Infraorder Steatornithes
      Family Steatornithidae
    Infraorder Caprimulges
      Family Nyctibiidae
          Caprimulgidae

Order Apodiformes
  Suborder Trochili
    Family Trochilidae
  Suborder Apodi
    Family Hemiprocnidae
        Apodidae

Division 9
Order Piciformes

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Suborder Galbulae
        Family Galbulidae
                Bucconidae
Suborder Pici
        Superfamily Capitonoidea
        Family Capitonidae
                Ramphastidae
        Superfamily Picoidea
        Family Indicatoridae
                Picidae

Order Coliiformes
        Family Coliidae

Order Coraciiformes
    Suborder Alcedines
        Infraorder Alcedini
            Superfamily Alcedinoidea
            Family Alcedinidae
                    Meropidae
            Superfamily Momotoidea
            Family Todidae
                    Momotidae
        Infraorder Coracii
            Superfamily Leptosomatoidea
            Family Leptosomatidae
            Superfamily Coracioidea
            Family Coraciidae
                    Brachypteraciidae
        Infraorder Trogones
            Family Trogonidae
    Suborder Upupes
            Family Upupidae
                    Phoeniculidae
    Suborder Bucerotes
            Family Bucerotidae

Order Passeriformes
    Suborder Tyranni
        Infraorder Eurylami
            Family Eurylaimidae
                    Philepittidae
        Infraorder Pitti
            Family Pittidae
        Infraorder Furnarii
            Superfamily Furnarioidea
            Family Dendrocolaptidae
                    Furnariidae
            Superfamily Formicarioidea
            Family Formicariidae
                    Rhinocryptidae
        Infraorder Tyrannomorpha
            Superfamily Tyrannoidea
            Family Cotingidae
                    Pipridae
                    Phytotomidae
                    Tyrannidae
                    Oxyruncidae
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Suborder Passeres
    Family Acanthisittidae, *incertae sedis*
        Alaudidae, *incertae sedis*
        Hirundinidae, *incertae sedis*
  Infraorder Muscicapi
    Family Prunellidae, *incertae sedis*
        Motacillidae, *incertae sedis*
    Superfamily Muscicapoidea
    Family Muscicapidae
     Subfamily Muscicapinae
        Turdinae
    Family Cinclidae
        Mimidae
        Troglodytidae
    Superfamily Sylvioidea
    Family Sylviidae
     Subfamily Sylviinae
        Timaliinae
        Monarchinae
        Malurinae
        Rhipidurinae
        Pachycephalinae
        Orthonychinae
        Platysteirinae

  Infraorder Lanii
    Family Laniidae
     Subfamily Malaconotinae
     Subfamily Laniinae
      Tribe Laniini
        Prionopini (inc. *Pityriasis*)
    Family Vangidae

  Infraorder Bombycilli
    Family Bombycillidae
     Subfamily Hypocoliinae
        Dulinae
        Bombycillinae
        Ptilogonatinae

  Infraorder Sitti
    Family Certhiidae
    Family Sittidae
     Subfamily Salpornithinae
        Sittinae
        Hyposittinae
    Family Paridae
     Subfamily Parinae
        Remizinae
        Aegithalinae

  Infraorder Meliphagi
    Family Dicaeidae
        Nectariniidae
        Meliphagidae
        Zosteropidae

  Infraorder Corvi
    Family Oriolidae, *incertae sedis*

        Dicruridae, *incertae sedis*
        Artamidae, *incertae sedis*
        Pycnonotidae, *incertae sedis*
        Irenidae, *incertae sedis*
        Campephagidae, *incertae sedis*
    Superfamily Menuroidea
      Family Menuridae
        Atrichornithidae
    Superfamily Corvoidea
      Family Grallinidae
        Corvidae
    Superfamily Sturnoidea
   Infrasuperfamily Cractici
     Family Cracticidae
   Infrasuperfamily Sturni
     Family Sturnidae
   [Family Callaeidae
   [Family Paradisaeidae
      Subfamily Ptilonorhynchinae
          Paradisaeinae

Infraorder Passeromorpha
    Superfamily Passeroidea
      Family Passeridae
  [Superfamily Ploceoidea
  [Family Ploceidae
  [Superfamily Estrildoidea
      Family Bubalornithidae
      Family Estrildidae
       Subfamily Poephilinae
           Estrildinae (inc. Viduini)

    Infraorder Fringilli
      Superfamily Vireonoidea
       Family Vireonidae
      Superfamily Emberizoidea
       Family Parulidae
    [Family Thraupidae
    [Family Emberizidae
       Subfamily Cardinalinae
       Subfamily Emberizinae
         Tribe Emberizini
           Icterini
       Subfamily Carduelinae
         Tribe Carduelini
           Drepanidini

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