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A CLASSIFICATION OF THE LIVING BIRDS OF THE WORLD BASED ON DNA-DNA HYBRIDIZATION STUDIES

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ABSTRACT.—We present a classification of the living birds of the world based on the results of DNA-DNA hybridization studies. Several family-group names are presented formally for the first time; some of these names have appeared earlier in various publications. *Received 21 January 1988, accepted 30 March 1988.*

THIS classification, and the phylogeny on which it is based, were first presented as posters at the XIX International Ornithological Congress in Ottawa, Canada, in June 1986, and later at the A.O.U. annual meetings in 1986 (Starkville, Mississippi) and 1987 (San Francisco, California). Figures 1–5 depict the branching pattern of the phylogeny above the level of subfamilies. Dendrograms of the complete DNA-based phylogeny will be included in a forthcoming book (Sibley and Ahlquist in prep.). We present the classification at this time because parts of it have been, or will be, used in works by other authors.

We believe that DNA-DNA hybridization comparisons provide data that may be used to reconstruct the branching pattern of the phylogeny of living birds. The delta $T_{50}H$ values (e.g. Sibley and Ahlquist 1981, 1983, 1986) are believed to be relative to time, but we no longer assume that there is a simple relationship between delta values and absolute time. Instead, it seems likely that the average rate of nucleotide substitution may be correlated with factors related to reproduction; for example, age at first breeding, generation time, number of cell divisions in the germline, and possibly other factors. This subject is discussed by Ahlquist et al. (1987), Catzeflis et al. (1987), Sibley and Ahlquist (1987d), and Sibley et al. (1987).

The dendrograms were constructed by the method of average linkage, or UPGMA (unweighted pair group method using arithmetic averages, Sneath and Sokal 1973: 230). The DNAs of 1,058 species, of which 310 were radio-labeled tracers, were used to reconstruct the phylogeny. Groups at and above the ordinal level were clustered from several overlapping matrices. For example, in the Passeriformes complete matrices were prepared for the suboscines, the Corvida and the Passerida, and among these matrices enough measurements were made to establish the positions of these groups relative to one another and to the non-passerines. The major groups were clustered on the basis of complete, or nearly complete, matrices consisting of the radio-labeled species. At least one species in each group in Figs. 1–5 was radio-labeled and reciprocals between nearly all branches were made. The averaging effect of UPGMA smooths out some of the effects of different average rates of genomic evolution, but relative rate tests were used to determine the branching order of taxa.

Hennig (1966: 160) proposed the age of origin as the ideal basis for the ranking of taxonomic categories. The application of this principle would produce a classification in which different lineages with the same age of origin would be placed in the same categorical rank, thus

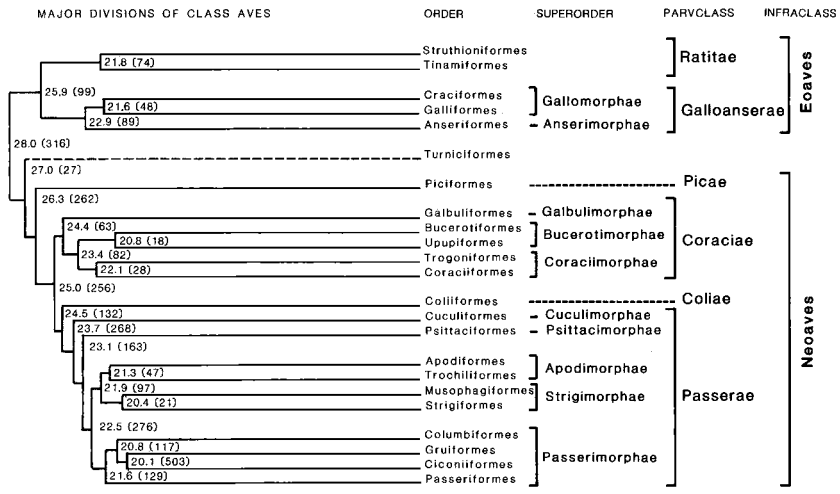

Fig. 1. Major divisions of the class Aves. The numbers, e.g. 28.0 (316), indicate that the average delta $T_{50}H$ value of 28.0 is based on the delta $T_{50}H$ values of 316 DNA-DNA hybrids between taxa on the two sides of the branch node.

achieving the desirable goal of *categorical equivalence.* Hennig (1966: 161–182) discussed the problems associated with determining the ages of origin of systematic groups and concluded that the available methods were inadequate. The present methods still fall short of the ideal, but we have tried to incorporate the principle of categorical equivalence into our classification by assigning ranks on the basis of delta $T_{50}H$ values (Table 1). The delta values express degrees of genomic divergence and, since the average rate of divergence is relative to time, this procedure provides an approach to categorical equivalence based on time of origin. The fact

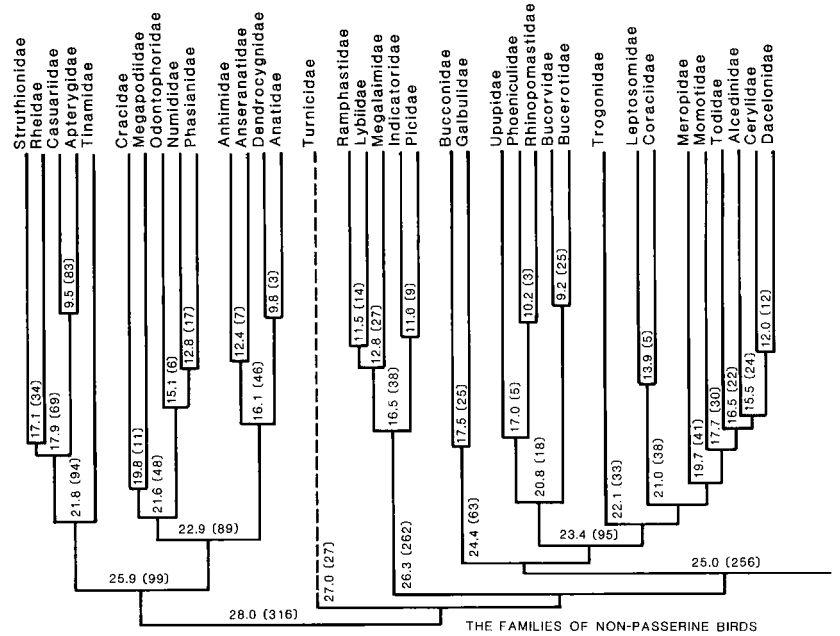

Fig. 2. Families of non-Passerine birds, Struthionidae to Dacelonidae.

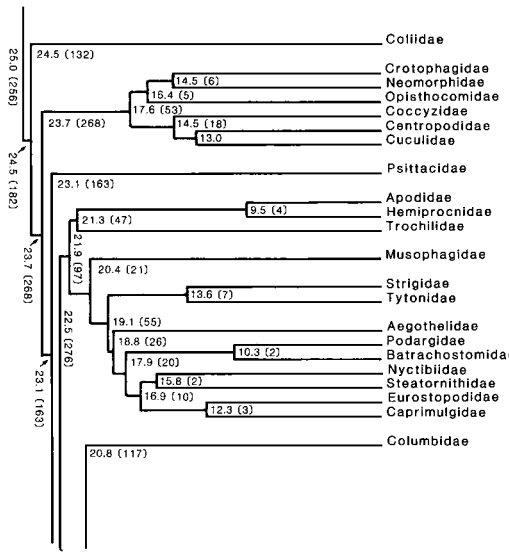

Fig. 3. Families of non-passerine birds, Coliidae to Columbidae.

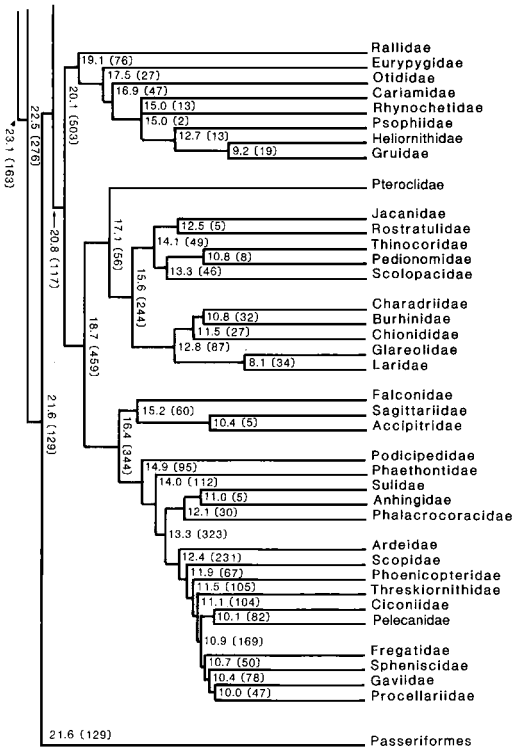

Fig. 4. Families of non-passerine birds, Rallidae to Procellariidae, and the position of the Passeriformes.

that different lineages evolve at somewhat different average rates introduces an error of uncertain magnitude.

The Turnicidae may present a special problem. The 27 delta $T_{50}H$ values between *Turnix* and other taxa are large, ranging from 22.7 to the pectoral sandpiper (*Calidris melanotos*) to 29.8 to the ostrich (*Struthio camelus*); average = 27.0. The range of 7.1 is unusually large. The smaller delta values are between *Turnix* and members of the Gruiformes and Charadriides; the larger delta values are between *Turnix* and the ratites, tinamous, galliforms and anseriforms. Members of several other non-passerine groups produced delta values between the extremes. Thus, *Turnix* seems to have no close living relatives, but *Turnix* species begin to breed at the age of three to five months (Bruning 1985), therefore it is possible that their average rate of genomic evolution is faster than the rate(s) among their nearest relatives. If so, the branch length we observe may be longer by an unknown factor and the correct position of the branch node may be elsewhere in the tree, possibly among the gruiforms where the Turnicidae have often been assigned. The problem is not insoluble, but will require additional comparisons and, perhaps, the development of a correction for different ages at first breeding. For now we leave the Turnicidae in the position indicated in Figs. 1 and 2, but designate the group as *incertae sedis*.

Does the *Turnix* problem cast doubt on the positions of all taxa in the tree? We think not, because nearly all other groups consist of many species and several levels of branchings, but the members cluster in spite of somewhat different ages at maturity. For example, members of the Procellariidae range in age at first breeding from ca. 3–4 years (Storm-Petrels) to more than 10 years (large albatrosses). Differences in branch lengths are revealed by relative rate tests, but all procellariids are closer to one another than to any outside group. Similarly, the estrildine finches begin to breed when less than one year of age, but they cluster with the other members of the Passeridae and are closest to the viduines, as expected.

Thus, it is possible that the Turnicidae are actually as isolated as their position in Figs. 1 and 2 suggests, but their exceptionally early maturity, and possible rapid DNA evolution, raise a question that must be considered, but cannot be resolved at this time.

Hennig (1966: 154–160) proposed that the sister branches at each dichotomy should receive

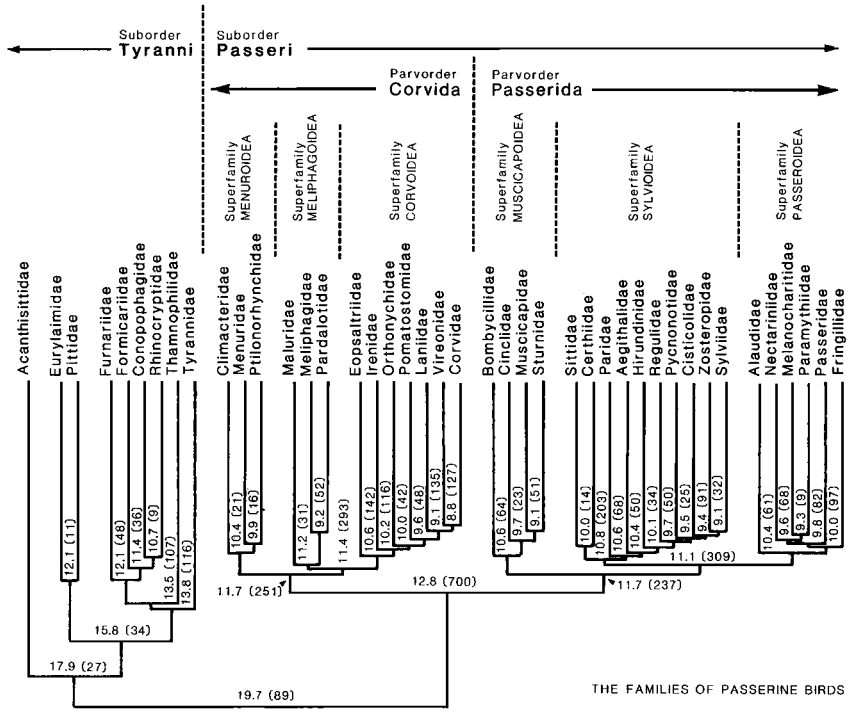

Fig. 5. Families of passerine birds.

the same categorical rank, and that each different level of branching should be assigned a different rank, arranged according to their relative age of origin. From Figs. 1–5 it is apparent that the DNA-based phylogeny contains numerous dichotomies at many levels and that it would be impractical to assign a different categorical name to every branch node in the phylogeny. Therefore, to accommodate the several branches that often occur within a single rank in our system, we have adopted the principles of "subordination and sequencing of units" proposed by Nelson (1973). If there are more than two branches within a taxonomic rank, the branch with the largest delta $T_{50}H$ value is listed first and is the sister group of the other branches; the lineage with the next largest delta value is listed next, etc. For dichotomous branchings the taxa are the same age and their positions in the dendrogram and classification are interchangeable. It has been necessary to be flexible in the assignment of categories and there are several places where a taxon may be adjusted up or down in rank. Thus, the classification attempts to reflect the branching pattern of the phylogeny, but does not claim to reproduce it in detail.

When the classification was first developed the categories were based on units of 10 million years and equated with delta $T_{50}H$ values on the basis of delta $T_{50}H$ 1.0 = 4.5 million years (e.g. Sibley and Ahlquist 1983, 1985a, b). It now seems likely that this calibration factor is not applicable to all birds, but only to those with ages at first breeding of ca. 2–4 years. Species that

TABLE 1. Categories, endings of categorical names, and delta $T_{50}H$ ranges for each categorical rank.

Category	Ending	Delta $T_{50}H$ range
Superclass	—	33–36
Class	—	31–33
Subclass	-ornithes	29–31
Infraclass	-aves	27–29
Parvclass	-ae	24.5–27
Superorder	-morphae	22–24.5
Order	-iformes	20–22
Suborder	-i	18–20
Infraorder	-ides	15.5–18
Parvorder	-ida	13–15.5
Superfamily	-oidea	11–13
Family	-idae	9–11
Subfamily	-inae	7–9
Tribe	-ini	4.5–7
Subtribe	-ina	2.2–4.5
Congeneric spp.	—	0–2.2

begin to breed at one year of age evolve slightly faster, and those that begin to breed at ages greater than four years evolve slightly slower. The differences in average genomic rates in birds seem to be small compared with the range in at least some other groups; for example, mammals, in which the rodents (Catzeflis et al. 1987) are evolving ca. ten times as fast as the hominoid primates (Sibley and Ahlquist 1987d).

Although we have changed the basis for categorical rank from absolute time to delta values, we have retained the delta $T_{50}H$ ranges originally assigned to the categories. We began by accepting the traditional rank of Class for the Aves and of Order for the Passeriformes. The delta $T_{50}H$ value for the passerine branch is 21.6 (Fig. 4), and the ordinal level became the range of values from delta $T_{50}H$ 20.0 to 22.2. The other ranks were developed above and below this level (Table 1). The application of this system to the proposed classification required four categories in addition to those traditionally used. These are Infraclass and Parvclass between Class and Order, and Infraorder and Parvorder between Order and Family. For consistency we have standardized the endings for the categories below the level of Class (Table 1). We have not used the Subtribe category. DNA hybridization data were available for most of the major groups of living birds. Those for which such data were lacking are listed as "*incertae sedis*" and placed in their traditional position, or in one suggested by data from other sources.

At first glance this classification may seem to be a radical departure from the familiar pattern of the Wetmore (1960) arrangement. For example, the "higher" non-passerines (woodpeckers, rollers, etc.) have become members of the "lower" non-passerines, and the waterbirds (except Anseriformes) have been moved in the opposite direction, from the beginning to the end of the non-passerine series. The order "Pelecaniformes" has been partially dismembered, and the New World vultures are allied to the storks, not to the Old World vultures. However, from a morphological study Cottam (1957) concluded that the pelicans and the Shoebill (*Balaeniceps rex*) are related, and the New World vultures and storks were considered close relatives by Garrod (1873) and Ligon (1967) (Sibley and Ahlquist 1985d: 125).

There is also a high degree of congruence between the DNA-based classification and the boundaries of the families and orders long recognized by avian systematists. Most of the traditional orders and ca. 90% of the families based on morphological similarities have also been delineated by the DNA comparisons, although their categorical ranks may have been changed. For example, the woodpeckers, honeyguides, barbets, and toucans cluster together; owls and goatsuckers are sister groups; the diverse gruiforms (to our surprise) remain mostly intact, and the charadriiforms are little changed except for modifications in rank. Grouse cluster with quails, ducks cluster with geese, motmots with kingfishers, hawks with eagles, pigeons with doves, hornbills with hoopoes, and cotingas with manakins. With few exceptions the DNA comparisons "see" the same clusters of species that are seen by the human eye.

The principal restructuring in the Passeriformes is the result of the division of the oscines (Passeri) into the parvorders Corvida and Passerida. The Corvida apparently evolved in Australia and New Guinea; the Passerida in Eurasia, Africa, and North America (Sibley and Ahlquist 1985b). This division is congruent with the distribution of at least one morphological character, namely, the condition of the tricipital fossa in the head of the humerus; the Corvida have a single fossa that is pneumatic, the Passerida have two fossae which are not pneumatic (Sibley and Ahlquist 1984a, 1987a; Olson 1987). These conditions are randomly distributed in relation to the Wetmore (1960) classification (Bock 1962).

Thus, the major differences between our classification and traditional arrangements are at the older levels where the higher categories are linked to one another. At these levels we should expect it to be more difficult to discern relationships from morphology because convergent and divergent evolution have had longer to introduce complexities into the interpretation of morphological characters. The DNA comparisons detect only the degrees of nucleotide sequence similarity which, we assume, are indices of genealogical relationships.

A phylogeny, and a classification based upon it, are hypotheses about the evolution of a group of organisms. Each segment of a classification is a hypothesis that may be tested by several methods, one of which is the degree of congruence with independent sources of evidence, as noted above. For example, Raikow (1987: 42) compared the phylogeny he derived from a study of the hindlimb musculature of the Old

World suboscines "... to one suggested by C. G. Sibley and co-workers from their studies on DNA-DNA hybridization. Although not identical, the results of the two studies are so similar that the agreement cannot be attributed to chance. Given the unrelated nature of the data used in these different studies, the correspondence between their results must be due to their independent determination of an approximation of the true historical phylogeny. The relationships proposed in both investigations differ markedly from those in earlier, more traditional studies."

There are additional examples of congruence and of incongruence between evidence from morphology and from DNA-DNA hybridization data, and there are many cases of disagreement between different studies based on morphology. Consensus has not yet been achieved, but the molecular methods provide new tools and concepts that are being incorporated into the procedures and philosophy of systematics.

We hope that further comparative studies will be made using this classification as the basis for new questions and hypotheses. We cannot guarantee, and we do not claim, that the classification is a true reflection of the phylogeny of living birds, but we believe that it represents progress toward that elusive goal.

Some of the new names for higher categories may seem inappropriate, for example, Passerimorphae for a group that includes pigeons, cranes, shorebirds, herons, hawks, albatrosses, and passerines. This, and all family-group names, are based on the first use of a generic root as the basis of a family name. Such names are not covered by the International Rules of Zoological Nomenclature, but we have used names that would be acceptable under the Rules. In this case Passeridae (Vigors 1825) happens to be the basis for the names of higher categories that include the Passeriformes.

The following publications include parts of the classification, some of the DNA-DNA hybridization data on which it is based, or both: Ahlquist et al. (1984), Sibley and Ahlquist (1981, 1982a, b; 1984a, b; 1985a–d; 1987a–d), and Sibley et al. (1982, 1984). These publications include citations to others that pertain to the classification.

CLASSIFICATION OF LIVING BIRDS OF THE WORLD

* = New family-group concept, combining one or more family groups.
** = First modern usage at family or superfamily level in DNA-DNA hybridization studies.
*** = New family-group name created in DNA-DNA hybridization studies.
# = New class-group or order-group name created in DNA-DNA hybridization studies (not covered by International Code of Zoological Nomenclature).

Class Aves
  Subclass Neornithes
    Infraclass Eoaves#
      Parvclass Ratitae
        Order Struthioniformes
          Suborder Struthioni
            Infraorder Struthionides
              Family Struthionidae, Ostrich
            Infraorder Rheides
              Family Rheidae, Rheas
          Suborder Casuarii
              Family Casuariidae
                Tribe Casuariini, Cassowaries
                Tribe Dromaiini, Emus
              Family Apterygidae, Kiwis
        Order Tinamiformes
              Family Tinamidae, Tinamous
      Parvclass Galloanserae#
        Superorder Gallomorphae
          Order Craciformes
            Suborder Craci

- Family Cracidae, Guans, Chachalacas, etc.
- Suborder Megapodii
  - Family Megapodiidae, Megapodes
- Order Galliformes
  - Parvorder Phasianida
    - Superfamily Phasianoidea
      - Family Phasianidae, Grouse, Pheasants, etc.
    - Superfamily Numidoidea
      - Family Numididae, Guineafowls
  - Parvorder Odontophorida
    - Family Odontophoridae, New World Quails
- Superorder Anserimorphae
  - Order Anseriformes
    - Infraorder Anhimides
      - Superfamily Anhimoidea
        - Family Anhimidae, Screamers
      - Superfamily Anseranatoidea
        - Family Anseranatidae, Magpie Goose
    - Infraorder Anserides
      - Family Dendrocygnidae, Whistling-Ducks
      - Family Anatidae
        - Subfamily Oxyurinae, Stiff-tailed Ducks
        - Subfamily Cygninae, Swans
        - Subfamily Anatinae
          - Tribe Anserini, Geese
          - Tribe Anatini, Typical Ducks

Infraclass?

- Order Turniciformes, *inc. sedis*
  - Family Turnicidae, Buttonquails = *Turnix, Ortyxelos*

Infraclass Neoaves

- Parvclass Picae
  - Order Piciformes
    - Infraorder Picides
      - Family Indicatoridae, Honeyguides
      - Family Picidae, Woodpeckers, Wrynecks
    - Infraorder Ramphastides
      - Superfamily Megalaimoidea
        - Family Megalaimidae,** Asian Barbets
      - Superfamily Lybioidea
        - Family Lybiidae,*** African Barbets
      - Superfamily Ramphastoidea
        - Family Ramphastidae*
          - Subfamily Capitoninae, New World Barbets
          - Subfamily Ramphastinae, Toucans
- Parvclass Coraciae
  - Superorder Galbulimorphae
    - Order Galbuliformes
      - Infraorder Galbulides
        - Family Galbulidae, Jacamars
      - Infraorder Bucconides
        - Family Bucconidae, Puffbirds
  - Superorder Bucerotimorphae
    - Order Bucerotiformes
      - Family Bucerotidae, Typical Hornbills
      - Family Bucorvidae, Ground-Hornbills
    - Order Upupiformes
      - Infraorder Upupides
        - Family Upupidae, Hoopoes

Infraorder Phoeniculides
Family Phoeniculidae, Wood-Hoopoes
Family Rhinopomastidae,*** Scimitarbills
Superorder Coraciimorphae
Order Trogoniformes
Family Trogonidae
Subfamily Apaloderminae, African Trogons
Subfamily Trogoninae
Tribe Trogonini, New World Trogons
Tribe Harpactini, Asian Trogons
Order Coraciiformes
Suborder Coracii
Superfamily Coracioidea
Family Coraciidae, Typical Rollers
Family Brachypteraciidae, Ground-Rollers (*inc. sedis*)
Superfamily Leptosomoidea
Family Leptosomidae, Cuckoo-Rollers
Suborder Alcedini
Infraorder Alcedinides
Parvorder Momotida
Family Momotidae, Motmots
Parvorder Todida
Family Todidae, Todies
Parvorder Alcedinida
Family Alcedinidae, Alcedinid Kingfishers
Parvorder Cerylida
Superfamily Dacelonoidea
Family Dacelonidae, Dacelonid Kingfishers
Superfamily Ceryloidea
Family Cerylidae, Cerylid Kingfishers
Infraorder Meropides
Family Meropidae, Bee-eaters
Parvclass Coliae
Order Coliiformes
Family Coliidae
Subfamily Coliinae, Typical Mousebirds
Subfamily Urocoliinae, Long-tailed Mousebirds**
Parvclass Passerae
Superorder Cuculimorphae
Order Cuculiformes
Infraorder Cuculides
Parvorder Cuculida
Superfamily Cuculoidea
Family Cuculidae, Old World Cuckoos
Superfamily Centropodoidea
Family Centropodidae,** Coucals
Parvorder Coccyzida
Family Coccyzidae,** American Cuckoos
Infraorder Crotophagides
Parvorder Opisthocomida
Family Opisthocomidae, Hoatzin
Parvorder Crotophagida
Family Crotophagidae
Tribe Crotophagini, Anis
Tribe Guirini,*** Guira Cuckoo
Parvorder Neomorphida
Family Neomorphidae, Roadrunners, etc.
Superorder Psittacimorphae
Order Psittaciformes

Family Psittacidae, Parrots, Macaws, etc.
Superorder Apodimorphae
Order Apodiformes
Family Apodidae, Typical Swifts
Family Hemiprocnidae, Crested Swifts
Order Trochiliformes
Family Trochilidae
Subfamily Phaethornithinae, Hermits
Subfamily Trochilinae, Typical Hummingbirds
Superorder Strigimorphae
Order Musophagiformes
Family Musophagidae
Subfamily Musophaginae, Turacos
Subfamily Criniferinae, Plaintain-eaters
Order Strigiformes
Suborder Strigi
Parvorder Tytonida
Family Tytonidae, Barn and Grass owls
Parvorder Strigida
Family Strigidae, Typical Owls
Suborder Aegotheli
Family Aegothelidae, Owlet-nightjars
Suborder Caprimulgi
Infraorder Podargides
Family Podargidae, Australian Frogmouths
Family Batrachostomidae,*** Asian Frogmouths
Infraorder Caprimulgides
Parvorder Steatornithida
Superfamily Steatornithoidea
Family Steatornithidae, Oilbird
Superfamily Nyctibioidea
Family Nyctibiidae, Potoos
Parvorder Caprimulgida
Superfamily Eurostopodoidea
Family Eurostopodidae,*** Eared Nightjars
Superfamily Caprimulgoidea
Family Caprimulgidae
Subfamily Chordeilinae, Nighthawks
Subfamily Caprimulginae, Nightjars
Superorder Passerimorphae
Order Columbiformes
Family Columbidae, Pigeons, Doves
Order Gruiformes
Suborder Grui
Infraorder Eurypygides
Family Eurypygidae, Sunbittern
Infraorder Otidides
Family Otididae, Bustards
Infraorder Gruides
Parvorder Gruida
Superfamily Gruoidea
Family Gruidae, Cranes
Family Heliornithidae
Tribe Aramini, Limpkin
Tribe Heliornithini, New World Sungrebe (*Podica* & *Heliopais inc. sedis*)
Superfamily Psophioidea
Family Psophiidae, Trumpeters
Parvorder Cariamida
Family Cariamidae, Seriemas

Family Rhynochetidae, Kagu
Suborder Ralli
Family Rallidae, Rails, Gallinules, Coots
Suborder Mesitornithi, *inc. sedis*
Family Mesitornithidae, Mesites
Order Ciconiiformes
Suborder Charadrii
Infraorder Pteroclides
Family Pteroclidae, Sandgrouse
Infraorder Charadriides
Parvorder Scolopacida
Superfamily Scolopacoidea
Family Thinocoridae, Seedsnipe
Family Pedionomidae, Plains-wanderer
Family Scolopacidae
Subfamily Scolopacinae, Woodcock, Snipe
Subfamily Tringinae, Sandpipers, Curlews, Phalaropes
Superfamily Jacanoidea
Family Rostratulidae, Paintedsnipe
Family Jacanidae, Lily-trotters, Jacanas
Parvorder Charadriida
Superfamily Chionidoidea
Family Chionididae, Sheathbills
Superfamily Charadrioidea
Family Burhinidae, Thickknees
Family Charadriidae
Subfamily Recurvirostrinae
Tribe Haematopodini, Oystercatchers
Tribe Recurvirostrini, Avocets, Stilts
Subfamily Charadriinae, Plovers, Lapwings
Superfamily Laroidea
Family Glareolidae
Subfamily Dromadinae, Crab-plover
Subfamily Glareolinae, Pratincoles
Family Laridae
Subfamily Larinae
Tribe Stercorariini, Jaegers, Skuas
Tribe Rynchopini, Skimmers
Tribe Larini, Gulls
Tribe Sternini, Terns
Subfamily Alcinae, Auks, Murres, Puffins
Suborder Ciconii
Infraorder Falconides
Parvorder Accipitrida
Family Accipitridae
Subfamily Pandioninae, Osprey
Subfamily Accipitrinae, Hawks, Eagles
Family Sagittariidae, Secretarybird
Parvorder Falconida
Family Falconidae, Falcons, Caracaras
Infraorder Ciconiides
Parvorder Podicipedida
Family Podicipedidae, Grebes
Parvorder Phaethontida
Family Phaethontidae, Tropicbirds
Parvorder Sulida
Superfamily Suloidea
Family Sulidae, Boobies, Gannets
Family Anhingidae, Anhingas

- Superfamily Phalacrocoracoidea
  - Family Phalacrocoracidae, Cormorants
- Parvorder Ciconiida
  - Superfamily Ardeoidea
    - Family Ardeidae, Herons, Bitterns, Egrets
  - Superfamily Scopoidea
    - Family Scopidae, Hammerhead
  - Superfamily Phoenicopteroidea
    - Family Phoenicopteridae, Flamingos
  - Superfamily Threskiornithoidea
    - Family Threskiornithidae, Ibises, Spoonbills
  - Superfamily Pelecanoidea
    - Family Pelecanidae
      - Subfamily Balaenicipitinae, Shoebill
      - Subfamily Pelecaninae, Pelicans
  - Superfamily Ciconioidea
    - Family Ciconiidae
      - Subfamily Cathartinae, New World vultures
      - Subfamily Ciconiinae, Storks
  - Superfamily Procellarioidea
    - Family Fregatidae, Frigatebirds
    - Family Spheniscidae, Penguins
    - Family Gaviidae, Loons
    - Family Procellariidae
      - Subfamily Hydrobatinae, Storm-Petrels
      - Subfamily Procellariinae, Shearwaters, Petrels, Diving-Petrels
      - Subfamily Diomedeinae, Albatrosses

Order Passeriformes

- Suborder Tyranni (Suboscines)
  - Infraorder Acanthisittides
    - Family Acanthisittidae, New Zealand Wrens
  - Infraorder Eurylaimides
    - Superfamily Pittoidea
      - Family Pittidae, Pittas
    - Superfamily Eurylaimoidea
      - Family Eurylaimidae, Broadbills
      - Family Philepittidae, Asities (*inc. sedis*)
  - Infraorder Tyrannides
    - Parvorder Tyrannida
      - Family Tyrannidae
        - Subfamily Corythopinae, *Corythopis, Mionectes,* etc.
        - Subfamily Tyranninae, Tyrant Flycatchers
        - Subfamily Tityrinae
          - Tribe Schiffornithini, *Schiffornis*
          - Tribe Tityrini, Tityras, Becards
        - Subfamily Cotinginae, Cotingas, Plantcutters, Sharpbills
        - Subfamily Piprinae, Manakins
    - Parvorder Thamnophilida
      - Family Thamnophilidae, Typical Antbirds
    - Parvorder Furnariida
      - Superfamily Furnarioidea
        - Family Furnariidae
          - Subfamily Furnariinae, Ovenbirds
          - Subfamily Dendrocolaptinae, Woodcreepers
      - Superfamily Formicarioidea
        - Family Formicariidae, Ground Antbirds
        - Family Conopophagidae, Gnateaters
        - Family Rhinocryptidae, Tapaculos
- Suborder Passeri (Oscines)

Parvorder Corvida
  Superfamily Menuroidea
    Family Climacteridae, Australo-Papuan Treecreepers
    Family Menuridae
      Subfamily Menurinae, Lyrebirds
      Subfamily Atrichornithinae, Scrubbirds
    Family Ptilonorhynchidae, Bowerbirds
  Superfamily Meliphagoidea
    Family Maluridae
      Subfamily Malurinae
        Tribe Malurini, Fairywrens
        Tribe Stipiturini, Emuwrens
      Subfamily Amytornithinae, Grasswrens
    Family Meliphagidae, Honeyeaters, incl. *Ephthianura, Ashbyia*
    Family Pardalotidae
      Subfamily Pardalotinae, Pardalotes
      Subfamily Dasyornithinae, Bristlebirds
      Subfamily Acanthizinae
        Tribe Sericornithini, Scrubwrens
        Tribe Acanthizini, Thornbills, Whitefaces, etc.
  Superfamily Corvoidea
    Family Eopsaltriidae, Australo-Papuan robins, *Drymodes*
    Family Irenidae, Fairy-bluebirds, Leafbirds
    Family Orthonychidae, Log-runners or Chowchillas
    Family Pomatostomidae,*** Australo-Papuan babblers
    Family Laniidae, True Shrikes = *Lanius, Corvinella, Eurocephalus*
    Family Vireonidae, Vireos, Greenlets, Peppershrikes
    Family Corvidae
      Subfamily Cinclosomatinae, Quail-thrushes, Whipbirds
      Subfamily Corcoracinae, Australian Chough, Apostlebird
      Subfamily Pachycephalinae
        Tribe Neosittini, Sittellas
        Tribe Mohouini, New Zealand *Mohoua, Finschia*
        Tribe Falcunculini, Shrike-tits, *Oreoica, Rhagologus*
        Tribe Pachycephalini, Whistlers, Shrike-thrushes
      Subfamily Corvinae
        Tribe Corvini, Crows, Magpies, Jays, Nutcrackers
        Tribe Paradisaeini, Birds of Paradise, *Melampitta*
        Tribe Artamini, Currawongs, Woodswallows, *Peltops, Pityriasis*
        Tribe Oriolini, Orioles, Cuckooshrikes
      Subfamily Dicrurinae
        Tribe Rhipidurini, Fantails
        Tribe Dicrurini, Drongos
        Tribe Monarchini, Monarchs, Magpie-larks
      Subfamily Aegithininae, Ioras
      Subfamily Malaconotinae
        Tribe Malaconotini, Bush-shrikes
        Tribe Prionopini, Helmet-shrikes, *Batis, Platysteira*, Vangas
    Family Callaeatidae, New Zealand wattlebirds (*inc. sedis*)
Parvorder Passerida
  Superfamily Muscicapoidea
    Family Bombycillidae
        Tribe Dulini, Palmchat
        Tribe Ptilogonatini, Silky-flycatchers
        Tribe Bombycillini, Waxwings
    Family Cinclidae, Dippers
    Family Muscicapidae
      Subfamily Turdinae, True thrushes, incl. *Chlamydochaera, Brachypteryx, Alethe*
      Subfamily Muscicapinae
        Tribe Muscicapini, Old World Flycatchers
        Tribe Saxicolini, Chats, *Erithacus*, etc.

- Family Sturnidae
  - Tribe Sturnini, Starlings, Mynas
  - Tribe Mimini, Mockingbirds, Thrashers, American Catbirds
- Superfamily Sylvioidea
  - Family Sittidae
    - Subfamily Sittinae, Nuthatches
    - Subfamily Tichodromadinae, Wallcreeper
  - Family Certhiidae
    - Subfamily Certhiinae
      - Tribe Certhiini, Northern Creepers
      - Tribe Salpornithini, Afro-Asian Creeper
    - Subfamily Troglodytinae, Wrens
    - Subfamily Polioptilinae, Gnatcatchers, Verdin, Gnatwrens
  - Family Paridae
    - Subfamily Remizinae, Penduline-Tits
    - Subfamily Parinae, Titmice, Chickadees
  - Family Aegithalidae, Long-tailed Tits, Bushtits
  - Family Hirundinidae
    - Subfamily Pseudochelidoninae, River-Martins (*inc. sedis*)
    - Subfamily Hirundininae, Swallows, Martins
  - Family Regulidae, Kinglets
  - Family Pycnonotidae, Bulbuls
  - Family Hypocoliidae, Gray Hypocolius (*inc. sedis*)
  - Family Cisticolidae, African Warblers
  - Family Zosteropidae, White-eyes
  - Family Sylviidae
    - Subfamily Phylloscopinae, Leaf Warblers
    - Subfamily Megalurinae, Grass Warblers, "*Bowdleria*" = *Megalurus*
    - Subfamily Garrulacinae, *Garrulax*
    - Subfamily Sylviinae
      - Tribe Timaliini, Babblers, *Picathartes*
      - Tribe Chamaeini, Wrentit
      - Tribe Sylviini, Sylviine Warblers
- Superfamily Passeroidea
  - Family Alaudidae, Larks
  - Family Nectariniidae
    - Subfamily Promeropinae, African Sugarbirds
    - Subfamily Nectariniinae
      - Tribe Dicaeini, Flowerpeckers
      - Tribe Nectariniini, Sunbirds, Spiderhunters
  - Family Melanocharitidae
    - Tribe Melanocharitini, *Melanocharis, Rhamphocharis*
    - Tribe Toxorhamphini, *Toxorhamphus, Oedistoma*
  - Family Paramythiidae, *Paramythia, Oreocharis*
  - Family Passeridae
    - Subfamily Passerinae, Sparrows, Rock-Sparrows, etc.
    - Subfamily Motacillinae, Wagtails and Pipits
    - Subfamily Prunellinae, Accentors, Dunnock
    - Subfamily Ploceinae, Weaverbirds, incl. *Amblyospiza, Bubalornis*, etc.
    - Subfamily Estrildinae
      - Tribe Estrildini, Waxbills, Estrildines
      - Tribe Viduini, Indigobirds, Whydahs
  - Family Fringillidae
    - Subfamily Peucedraminae, Olive Warbler
    - Subfamily Fringillinae
      - Tribe Fringillini, Chaffinches, Brambling
      - Tribe Carduelini, Goldfinches, Crossbills, etc.
      - Tribe Drepanidini, Hawaiian Honeycreepers
    - Subfamily Emberizinae
      - Tribe Emberizini, Buntings, Longspurs, Towhees
      - Tribe Parulini, Wood Warblers, incl. *Zeledonia*

Tribe Thraupini, Tanagers, Swallow-tanager, Neotropical Honeycreepers, Plushcap, Tanager-finches
Tribe Cardinalini, Cardinals
Tribe Icterini, Troupials, Meadowlarks, American Blackbirds, Oropendolas

NEW FAMILY-GROUP TAXA

Family Lybiidae, African Barbets (Sibley and Ahlquist 1985b). Type-Genus: *Lybius* Hermann 1783.

Family Rhinopomastidae, Scimitarbills (Sibley and Ahlquist 1985b). Type-Genus: *Rhinopomastus* Jardine 1828.

Tribe Guirini, Guira Cuckoo. Type-Genus: *Guira* Lesson 1830.

Family Batrachostomidae, Asian Frogmouths. Type-Genus: *Batrachostomus* Gould 1838.

Family Eurostopodidae, Eared Nightjars (Sibley and Ahlquist 1985b). Type-Genus: *Eurostopodus* Gould 1838.

Family Pomatostomidae, Australo-Papuan Babblers (Sibley and Ahlquist 1985b). Type-Genus: *Pomatostomus* Cabanis 1851.

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LITERATURE CITED

AHLQUIST, J. E., A. H. BLEDSOE, F. H. SHELDON, & C. G. SIBLEY. 1987. DNA hybridization and avian systematics. Auk 104: 556–563.

———, F. H. SHELDON, & C. G. SIBLEY. 1984. The relationships of the Bornean Bristlehead (*Pityriasis gymnocephala*) and the Black-collared Thrush (*Chlamydochaera jefferyi*). J. Ornithol. 125: 129–140.

BOCK, W. 1962. The pneumatic fossa of the humerus in the Passeres. Auk 79: 425–443.

BRUNING, D. 1985. Buttonquail. Pp. 76–77 *in* A dictionary of birds (B. Campbell and E. Lack, Eds.). Calton, England, T. and A. D. Poyser, Ltd.

CATZEFLIS, F. M., F. H. SHELDON, J. E. AHLQUIST, & C. G. SIBLEY. 1987. DNA-DNA hybridization evidence of the rapid rate of muroid rodent DNA evolution. Mol. Biol. Evol. 4: 242–253.

COTTAM, P. 1957. The pelecaniform characters of the skeleton of the shoe-bill stork, *Balaeniceps rex*. Zool. Bull. Brit. Mus. (Nat. Hist.) 5: 51–72.

GARROD, A. H. 1873. On certain muscles of the thigh of birds and on their value in classification, part I. Proc. Zool. Soc. London, 1873 [1874]: 626–644.

HENNIG, W. 1966. Phylogenetic systematics. Urbana, Univ. Illinois Press.

LIGON, J. D. 1967. Relationships of the cathartid vultures. Occasional Papers Univ. Michigan Mus. Zool. No. 651: 1–26.

NELSON, G. J. 1973. Classification as an expression of phylogenetic relationships. Syst. Zool. 22: 344–359.

OLSON, S. L. 1987. The relationships of the New Guinean ground-robins *Amalocichla*. Emu 87: 247–248.

RAIKOW, R. J. 1987. Hindlimb myology and evolution of the Old World suboscine passerine birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae). Ornithol. Monogr. No. 41. Washington, D.C., Amer. Ornithol. Union.

SIBLEY, C. G., & J. E. AHLQUIST. 1981. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301–335 *in* Evolution Today, Proc. 2nd. Intl. Congr. Syst. and Evol. Biol. (G. G. E. Scudder and J. L. Reveal, Eds.). Pittsburgh, Hunt Inst. Botanical Documentation, Carnegie-Mellon Univ.

———, & ———. 1982a. The relationships of the Hawaiian honeycreepers (Drepaninini) as indicated by DNA-DNA hybridization. Auk 99: 130–140.

———, & ———. 1982b. The relationships of the vireos (Vireoninae) as indicated by DNA-DNA hybridization. Wilson Bull. 94: 114–128.

———, & ———. 1983. The phylogeny and classification of birds based on the data of DNA-DNA hybridization. *In* Current Ornithology 1: 245–292 (R. F. Johnston, Ed.). New York and London, Plenum Press.

———, & ———. 1984a. The relationships of the starlings (Sturnidae: Sturnini) and the mockingbirds (Sturnidae: Mimini). Auk 101: 230–243.

———, & ———. 1984b. The relationships of the Papuan genus *Peltops*. Emu 84: 181–183.

———, & ———. 1985a. (publ. 1986). The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. Pp. 83–121 *in* Proc. 18th Intl. Ornithol. Congress, Moscow 1982 (V. D. Ilyichev and V. M. Gavrilov, Eds.). Moscow, Nauka Publ.

———, & ———. 1985b. The phylogeny and classification of the Australo-Papuan passerine birds. Emu 85: 1–14.

———, & ———. 1985c. The phylogeny and classification of the New World suboscine passerine birds (Passeriformes: Oligomyodi: Tyranni). Pp. 396–428 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Washington, D.C. Amer. Ornithol. Union Monograph No. 36.

———, & ———. 1985d. The relationships of some groups of African birds, based on comparisons of the genetic material, DNA. Pp. 115–161 *in* Proc. Symp. on African Vertebrates (K.-L. Schuchmann, Ed.). Bonn, Mus. A. Koenig.

———, & ———. 1986. Reconstructing bird phylogeny by comparing DNA's. Sci. Amer. 254: 82–92.

———, & ———. 1987a. Avian phylogeny reconstructed from comparisons of the genetic material, DNA. Pp. 95–121 *in* Molecules and morphology in evolution: conflict or compromise (C. Patterson, Ed.). London, Cambridge Univ. Press.

———, & ———. 1987b. The Lesser Melampitta is a bird of paradise. Emu 87: 66–68.

———, & ———. 1987c. The relationships of four species of New Zealand passerine birds. Emu 87: 63–66.

———, & ———. 1987d. DNA hybridization evidence of hominoid phylogeny: results from an expanded data set. J. Mol. Evol. 26: 99–121.

———, & ———. In prep. Phylogeny and classification of the birds of the world: a study in molecular evolution. New Haven, Yale Univ. Press.

———, ———, & F. H. Sheldon. 1987. DNA hybridization and avian phylogenetics. Reply to Cracraft. Pp. 97–125 *in* Evolutionary biology, vol. 21 (M. K. Hecht, B. Wallace, and G. T. Prance, Eds.). New York and London, Plenum Press.

———, R. SCHODDE, & J. E. AHLQUIST. 1984. The relationships of the Australo-Papuan treecreepers Climacteridae as indicated by DNA-DNA hybridization. Emu 84: 236–241.

———, G. R. WILLIAMS, & J. E. AHLQUIST. 1982. The relationships of the New Zealand wrens (Acanthisittidae) as indicated by DNA-DNA hybridization. Notornis 29: 113–130.

SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical taxonomy. San Francisco, W. H. Freeman.

VIGORS, N. A. 1825. Sketches in ornithology; or, observations on the leading affinities of some of the more extensive groups of birds. Arrangement of genera of birds. Zool. J. 2: 368–405.

WETMORE, A. 1960. A classification for the birds of the world. Smithson. Misc. Coll. 139 (11): 1–37.

On 25 April 1988, the ***Daniel Giraud Elliot Medal*** was awarded jointly to **Charles G. Sibley** (San Francisco State University; Professor Emeritus, Yale University) and **Jon Edward Ahlquist** (Department of Zoological and Biomedical Sciences, Ohio University). "Their massive, insight-rich application of DNA hybridization techniques to bird classification revolutionized taxonomy by showing at last how to distinguish avian evolutionary relationships from convergent similarities."

The prize was established in 1917 through the Daniel Giraud Elliot Fund by a gift from Margaret Henderson Elliot. It is awarded by the **National Academy of Sciences** for meritorious work in zoology or paleontology published over a three- to five-year period.