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**The Relationships of the
Yellow-breasted Chat (*Icteria virens*)
and the Alleged Slowdown in
the Rate of Macromolecular Evolution
in Birds**

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(Received 14 May 1981)

Abstract

The taxonomic relationships of the Yellow-breasted Chat (*Icteria virens*) have been uncertain since its discovery more than 200 years ago. Although usually considered to be a New World wood warbler (Parulini) it possesses structural and behavioral characteristics that seem aberrant in comparison with the typical members of that group. The relationships of *Icteria* were investigated by comparing its single-copy DNA sequences with those of other New World nine-primaried oscines and representatives of other oscine families, using the technique of DNA-DNA hybridization. The data indicate that *Icteria* is a paruline warbler and it should continue to be included within that group.

The study of *Icteria* provided the basis for an examination of the suggestion by several authors that the proteins of birds and, by extension, their DNAs, evolve more slowly than do those of other animals. Evidence is presented indicating that the alleged differences are due, at least in part, to differences in the human perception of the boundaries of taxonomic categories in birds versus most other organisms. Birds are taxonomically oversplit at all supra-

specific levels, but small, nocturnal mammals and other groups are probably overlumped at all levels. The lack of equivalence between the taxonomic categories of birds and those of other animals results in an erroneous evaluation of their rates of macromolecular evolution. DNA hybridization data indicate that the vireos (Vireoninae) are not closely related to the wood warblers, or to other New World nine-primaried oscines. We have shown elsewhere that the vireos are members of a large, varied "corvine assemblage."

Key Words

DNA-DNA hybridization, birds, Yellow-breasted Chat, macromolecular evolution, rate slowdown, avian systematics, categorical equivalence.

Introduction

The Yellow-breasted Chat (*Icteria virens*) breeds from southern Canada and the United States to central Mexico (Jalisco). It has been included among the New World wood warblers (Fringillidae:Emberizinae:Parulini, cf. Sibley, 1970; Sibley and Ahlquist, in press, a,c) for more than a century but its affinities repeatedly have been questioned because it is aberrant in comparison with the other species assigned to that group. *Icteria* is larger than any of the typical wood warblers and it differs from them in several structural and behavioral characters. Although it is a New World nine-

primaried oscine, it does not fit readily into any of the subgroups of that large assemblage.

Baird (1858) was the first to assign *Icteria* to the wood warblers and (p. 248) he noted the controversy surrounding it.

The proper position of this genus has always been a matter of much uncertainty, but I see no reason why it may not legitimately be assigned to the *Sylvicolinae*, possessing, as it does, so many of their characteristics. The bill is stouter and more curved than in the rest, but the other characters agree very well. It cannot properly be placed with the vireos and shrikes on account of the absence of a spurious primary, as well as of a notch in either mandible.

But the doubts soon returned. Coues (1892:311) questioned whether *Icteria* is "most naturally classed with the Warblers" and Newton (1896:85) noted that *Icteria* "is generally referred to the Family Mniotiltidae, or American Warblers, but may possibly not belong to them, its stout bill being very unlike that possessed by the rest." However, Baird's opinion was supported by Ridgway (1902:426) who wrote that

The position of *Icteria* in the Mniotiltidae has more than once been questioned; indeed it had not been referred to this family at all until 1858, when Professor Baird formally placed it here as sole representative of a group or section *Icterieae*. That he was fully justified in doing so is quite certain, for, however unlike other North American Mniotiltidae *Icteria* may seem, the extralimital genera *Chamaethlypis* and *Granatellus* distinctly connect it with more typical forms, the former being, indeed, a very near relative, its close relationship being shown even in the coloration.

Bent (1953:587) noted that "Audubon classed [*Icteria*] with the manakins, and others have placed it with the vireos or with the honeycreepers, but structurally it seems to be most closely related to the wood warblers. . . ." The fifth edition of the American Ornithologists' Union Check-list (1957) placed *Icteria* between *Chamaeth-*

lypis and *Euthlypis*, without even a footnote, and its acceptance as a paruline seemed to be settled, but not for long.

Eisenmann (1962) reopened the debate by questioning the validity of *Chamaethlypis* as distinct from *Geothlypis* and suggested these two genera be merged. Part of his argument related to Ridgway's (1902) statement that *Icteria* was linked to the typical parulines via *Chamaethlypis* and *Granatellus*. Eisenmann sought, and found, support for the idea that "Recent anatomical studies strongly suggest that *Icteria* is probably out of place in the wood-warblers." The evidence cited by Eisenmann included "in litt." communications from W. J. Beecher, who noted that a reexamination of his notes on the jaw musculature of *Icteria* showed that it "could be a tanager"; from William George, who reported that, in certain aspects, the hyoid apparatus of *Icteria* "differs markedly" from that of "all continental genera traditionally included in the Parulidae," as well as from that of "numerous genera of tanagers and other Oscines"; and from C. G. Sibley who advised Eisenmann "that the electrophoretic patterns of the egg-white proteins" of *Icteria* "are strikingly different" from those of the "typical" warblers and tanagers that were examined.

Eisenmann's paper stimulated Ficken and Ficken (1962) to add to the evidence that "the Yellow-breasted Chat is not properly classified as a parulid." They cited as "aberrant characters" of *Icteria* its nest structure, eggs, lack of natal down, complete post-juvinal molt ("which also occurs in *Geothlypis trichas*, but not in most other warblers"), color of mouth lining, song characteristics, nocturnal singing, courtship display, lack of a distraction display, and the habit of holding food with its feet. They concluded that "the Chat is not a parulid, but that its true relationships remain obscure."

These observations served to reopen the debate about the relationships of *Icteria*, although it now seems clear that the senior author provided Eisenmann with erroneous information in 1962. We do not now recall the basis for the statement quoted by Eisen-

mann (1962) but an examination of the electrophoretic patterns of the groups in question (Sibley, 1970, fig. 28), reveals that those of *Icteria* match those of the paruline warblers and other New World nine-primaried oscines, rather than being "strikingly different" from them.

New data on this problem have been presented by Avise et al. (1980a) from electrophoretic comparisons of 16 proteins in 28 species representing 12 genera of paruline warblers (including *Icteria*), a thrush (*Catharus ustulatus*), and a vireo (*Vireo olivaceus*). They found that *Icteria*, although the most distinctive of the wood warblers, is closer to them than to the thrush or the vireo.

In this paper we report the results of comparisons among the homologous nucleotide sequences of the single-copy DNAs of *Icteria virens* and representative genera of the wood warblers (Parulini), the tanagers (Thraupini), the buntings (Emberizini), the New World blackbirds (Icterini), the cardueline finches (Carduelini), the vireos (Vireonidae), the mimic thrushes (Muscicapidae: Mimini) and the wrens (Troglodytidae). These taxonomic allocations follow Sibley (1970) and Sibley and Ahlquist (1980; in press, a,b,c,e,f).

In addition, we doubt the interpretation of the evidence that has been presented purporting to show that the proteins, and presumably also the DNAs, of birds evolve more slowly than do those of mammals and reptiles.

Methods

The genetic material, DNA (deoxyribonucleic acid), is composed of two linear chains of four kinds of subunits called nucleotides. The four types of nucleotides differ in the structures of their "bases," which are adenine (A), guanine (G), thymine (T), and cytosine (C). In double-stranded DNA the four bases occur as complementary pairs, an adenine in one chain can pair only with a thymine in the other, a guanine can pair only with a cytosine. This A-T and

G-C base pairing results in the two single strands being complementary nucleotide sequences of one another. Genetic information is encoded in the sequence of the bases in the DNA strands.

In this paper the word "homologous" is used with two meanings. As applied to nucleotide sequences it means that two sequences, or genes, are the descendants of the same sequence in the common ancestral species. This equals the "orthologous" type of homology of Fitch (1976:161), defined as two different genes "whose difference is a consequence of independence arising from speciation. . . because there is an exact phyletic correspondence between the history of the genes and the history of the taxa from which they derive." Homologous, as applied to DNA-DNA hybrids, means a homoduplex hybrid composed of labeled and unlabeled DNA of the same species. Heterologous (or heteroduplex) hybrids are composed of DNAs from two different species.

The DNA hybridization technique takes advantage of the complementary structure of the double-stranded DNA molecule. When double-stranded DNA in solution is heated to ca. 100°C the hydrogen bonds between A-T and G-C base pairs dissociate and the two strands separate. Under proper conditions of temperature and salt concentration the two single strands will reassociate as the solution cools because the complementary bases "recognize" one another. If the temperature is maintained at a high enough level, e.g., 60°C, complementary base pairing will occur only between long homologous sequences of nucleotides. This is because only long sequences of complementary bases will have sufficient bonding strength to form stable duplexes at that temperature, and only homologous sequences possess the necessary degree of complementarity. Thus, under appropriate conditions of temperature and salt concentration, conspecific double-stranded DNA may be thermally dissociated and, because of their inherent properties, the single strands will reassociate only with their homologous partners.

Similarly, if the single-stranded DNAs of two different species are combined under conditions favoring reassociation hybrid double-stranded molecules will form between homologous sequences. These sequences will contain mismatched bases as a result of the nucleotide sequence differences that have evolved since the two species diverged from their most recent common ancestor. The lower bonding strength of such hybrid duplexes will cause them to dissociate at a temperature lower than that required to melt conspecific double-stranded DNA. Thus the property of sequence recognition exhibited by homologous sequences and the decreased thermal stability of imperfectly matched hybrid sequences form the basis of the DNA-DNA hybridization technique.

The extent of base pair matching between the homologous nucleotide sequences of any two DNAs can be determined by measuring (1) the percentage of hybridization and (2) the thermal stability of the reassociated duplex molecules. Following is a synopsis of the technique which is described in more detail by Sibley and Ahlquist (1981).

Nuclear DNAs from avian erythrocytes were purified (Marmur 1961, Shields and Straus 1975), sheared to an average fragment length of ca. 500 nucleotides by sonication, and sized by electrophoretic comparison with DNA fragments of known size produced by the digestion of bacteriophage DNA with bacterial restriction endonucleases (Nathans and Smith 1975). Single-copy DNA was prepared consisting of one copy per genome of each single-copy sequence, plus *at least* one copy per genome of each repeated sequence. Such a preparation contains more than 98% of the "complexity" of the genome, i.e., the total length of *different* DNA sequences (Britten 1971). Kohne (1970:333-347) discussed the method and reasons for removing the extra copies of repeated sequences in studies designed to determine "the extent of nucleotide change since the divergence of two species" (p. 347). We removed the excess repetitive sequences by reassociat-

ing the single-stranded DNA of the species to be "labeled" with radioiodine to a C_0t value of 1000 at 50°C in 0.48M sodium phosphate buffer (C_0t = the initial concentration of DNA in moles per liter times the time of incubation in seconds). (Kohne 1970:334).

The single-copy sequences were labeled with radioactive iodine (^{125}I) according to the procedures of Commorford (1971) and Prensky (1976). DNA-DNA hybrids were formed from a mixture composed of one part (=250 ng) ^{125}I -labeled single-copy DNA and 1000 parts (=250 μg) of sheared, whole DNA at a concentration of 2 mg/ml in 0.48 M sodium phosphate buffer. The hybrid combinations were heated to 100°C for 10 min to dissociate the double-stranded molecules into single strands, then incubated for at least 120 h (= C_0t 16,000) at 60°C to permit the single strands to form double-stranded hybrid molecules.

The hybrids were bound to hydroxyapatite columns immersed in a temperature-controlled water bath at 55°C and the temperature was then raised in 2.5°C increments from 55°C to 95°C. At each of the 17 temperatures the single-stranded DNA was eluted in 20 ml of 0.12M sodium phosphate buffer.

The radioactivity in each eluted sample was counted in a Packard Model 5220 Auto-Gamma Scintillation Spectrometer, optimized for ^{125}I . A teletype unit connected to the gamma counter printed out the data and punched a paper tape which is the entry to the computer program.

The computer program used a nonlinear regression least squares procedure to determine the best fit of the experimental data to one of four functions: 1) the Normal, 2) the dual-Normal, 3) the "skewed" Normal, or 4) a modified form of the Fermi-Dirac equation. The modal temperatures for each hybrid were calculated from the fitted curves. The differences (in °C) between the mode of the homologous hybrid, and that of a heterologous hybrid is the delta mode.

Results

Table 1 contains the delta mode values and Figure 1 is a diagram constructed from them. The delta mode values are measurements between the labeled species and the other species in Table 1, but not among the other species. However, two species that have the same delta mode value are equidistant from the labeled taxon, but they can be any distance from one another which is equal to, or less than, their common distance from the labeled species.

The data indicate that *Icteria* is most closely related to the wood warblers (*Geothlypis*, *Vermivora*, *Dendroica*), and that the tanagers (*Tangara*, *Ramphocelus*), the bunting (*Zonotrichia*), the grackle (*Quiscalus*), and the cardueline (*Carpodacus*) are progressively more distant. These genera are members of the Fringillidae as defined by Sibley (1970), and Sibley and Ahlquist (in press, a, c, e, f). The vireo, the catbird, and the wren are still more distant from *Icteria*. Because *Icteria* is a vocal mimic it has been proposed that it might be related to the mockingbirds (Mimidae), but the *Icteria:Dumetella* delta mode value of 11.0 indicates that the two taxa are as distant from one another as *Icteria* is from the wrens (11.9) or, as reported by Sibley and Ahlquist (in press, a), as *Himatione* is from *Sturnus*, *Monarcha*, *Turdus*, *Sylvia*, *Vireo*, and *Corvus*, which differ from *Himatione* by delta modes from 10.2 to 11.0 (average = 10.7).

The DNA hybridization data indicate that *Icteria* is a wood warbler, although it must represent an early branch in the phylogeny of the group. Its atypical anatomical and behavioral characters should be viewed as adaptive specializations, not as evidence that *Icteria* is more closely related to some group other than the Parulini.

The vireos have been thought to be closely related to the New World nine-primaried oscines at least since 1930, when Wetmore placed them next to the New World nine-primaried groups. Table 1 includes a DNA hybrid between *Icteria* and

the Red-eyed Vireo (*Vireo olivaceus*) which has a delta mode value of 10.4. Similarly, in our study of the Hawaiian honeycreepers (Fringillidae:Carduelinae:Drepaninini) a DNA hybrid between the Apapane (*Himatione sanguinea*) and the Red-eyed Vireo had a delta mode of 11.3 (Sibley and Ahlquist, in press, a). These data indicate that *Vireo* is not closely related to the New World nine-primaried assemblage. Avise et al. (1980a) presented evidence that *Vireo* is even more distant from the paruline warblers than are the turdine thrushes, represented by the Swainson's Thrush (*Catharus ustulatus*).

A DNA hybridization study in which *Vireo olivaceus* was the radioiodine-labeled taxon has shown that the typical vireos (*Vireo*, *Hylophilus*), the pepper-shrikes (*Cyclarhis*) and, presumably, the shrike-vireos (*Vireolanus*) are closely related to one another, and are not closely related to the American nine-primaried groups. Instead, they are members of a large, varied, "corvine assemblage" that includes the corvids, monarch flycatchers, cuckoo-shrikes, oriolids, birds-of-paradise, wood swallows, cracticids, drongos, and shrikes. The DNA hybrids between *Vireo* and members of these groups have delta values between 7.5 and 9.4 (Sibley and Ahlquist, in press, c). Additional data pertaining to the "corvine assemblage" are included in Sibley and Ahlquist (in press, d, g, h, i).

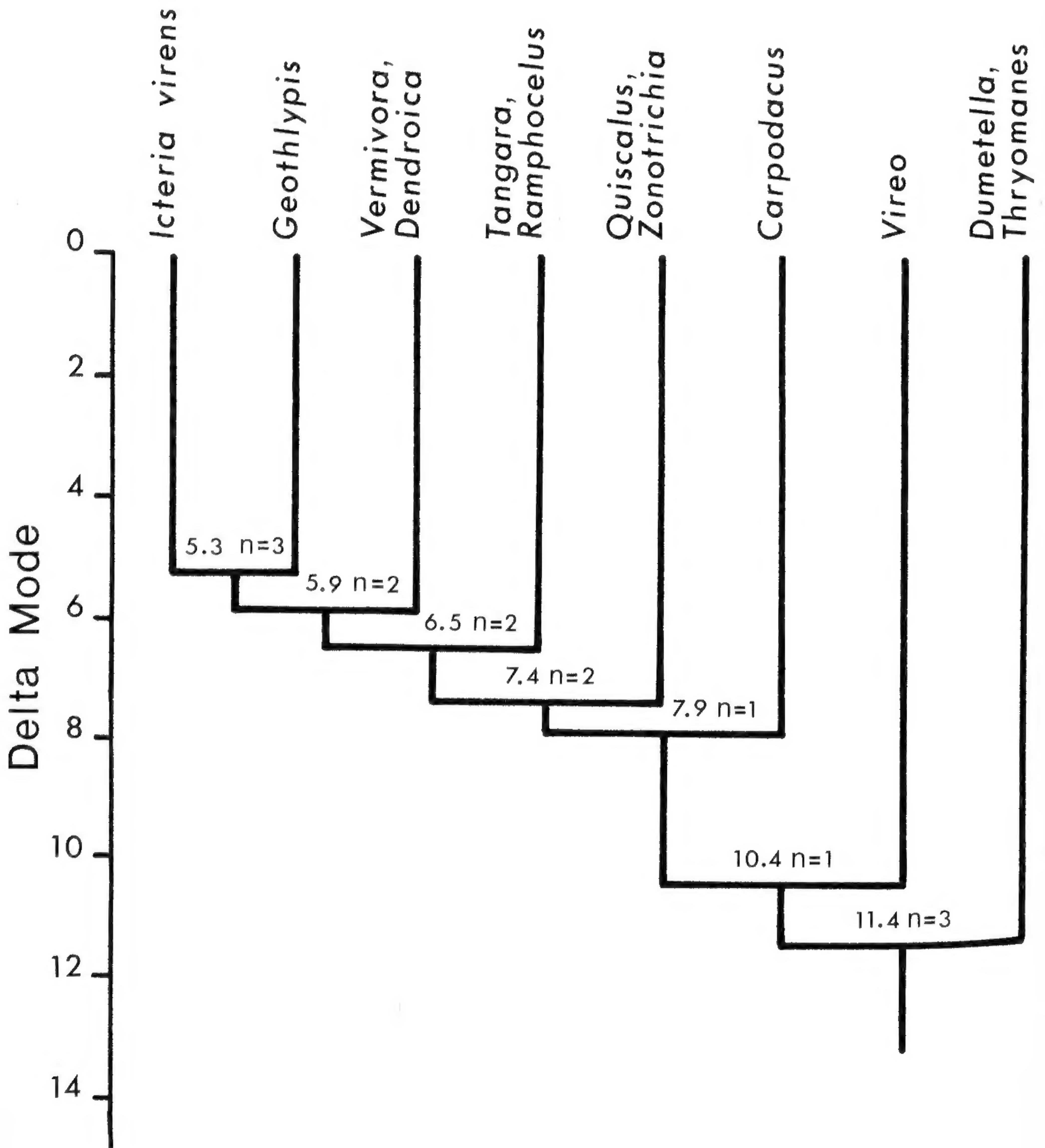
**Fig. 1**

Diagram based on the delta mode values given in Table 1. Because only the DNA of the Yellow-breasted Chat was labeled with radioactive iodine, the diagram depicts only the distances between it and the other taxa and not among those taxa.

Table 1.

Modal and delta modal values for DNA-DNA hybrids between the radioiodine (^{125}I)-labeled DNA of the Yellow-breasted Chat and the DNAs of some other passerine birds.

COMMON NAME	SCIENTIFIC NAME	MODE	Δ MODE
Yellow-breasted Chat	<i>Icteria virens</i>	85.8	0.0
Common Yellow-throat	<i>Geothlypis trichas</i>	80.5	5.3
Tennessee Warbler	<i>Vermivora peregrina</i>	80.0	5.8
Magnolia Warbler	<i>Dendroica magnolia</i>	79.8	6.0
Scrub Tanager	<i>Tangara vitriolina</i>	79.3	6.5
Silver-beaked Tanager	<i>Ramphocelus carbo</i>	79.2	6.6
Song Sparrow	<i>Zonotrichia melodia</i>	78.4	7.4
Common Grackle	<i>Quiscalus quiscula</i>	78.3	7.5
Purple Finch	<i>Carpodacus purpureus</i>	77.9	7.9
Red-eyed Vireo	<i>Vireo olivaceus</i>	75.4	10.4
Gray Catbird	<i>Dumetella carolinensis</i>	74.8	11.0
Bewick's Wren	<i>Thryomanes bewickii</i>	73.9	11.9

Discussion

Icteria is but one of many avian genera whose relationships have been unclear. The Wrenthrush, *Zeledonia coronata*, was considered to be a turdine thrush until the electrophoretic pattern of its egg white proteins revealed its relationship to the wood warblers (Sibley, 1968), and the Swallow-tanager, *Tersina viridis*, often placed in a monotypic family, is clearly a somewhat modified tanager (Sibley, 1973). The Hoatzin (*Opisthocomus*) was placed in the Galliformes because of its superficial similarity to the chachalacas (*Ortalis*), but its egg white proteins (Sibley and Ahlquist, 1973) revealed its cuculiform affinities. There are many additional examples of morphologically distinctive species of birds which have been viewed as taxonomically distant from their closest relatives. The discrepancy between our perception of taxonomic relationships based upon visible morphological characters, and evidence of relationships derived from comparisons of proteins and/or DNAs, deserves careful scrutiny, for it has important implications for systematic and evolutionary biology. One of the manifestations of this problem is the debate as to whether or not avian protein molecules evolve more slowly than do those of other animals.

One of the most interesting and controversial discoveries in recent years has been evidence that the amino acid sequences of proteins and the nucleotide sequences of DNA evolve at remarkably uniform average rates. The concept of the "molecular clock," first proposed by Zuckerkandl and Pauling (1962), has been discussed by many authors, including Fitch (1976), Wilson et al. (1977), and Doolittle (1979). We have found evidence for a uniform *average* rate of DNA evolution (i.e., nucleotide substitution) in our studies of the ratites (Sibley and Ahlquist, 1981), the Hawaiian honeycreepers (Sibley and Ahlquist, in press, a), the New Zealand Wrens (Sibley, Williams, and Ahlquist, in press), the vireos (Sibley and Ahlquist, in press, c) and the Australian fairy-wrens (Sibley and Ahlquist, in press, h).

Although there is considerable evidence that DNA and proteins evolve at constant or uniform *average* rates, several studies have led their authors to suggest that the proteins of birds may evolve more slowly than do those of other animals (Prager et al., 1974; Prager and Wilson, 1975; Barrowclough and Corbin, 1978; Avise et al., 1980a, b).

Prager et al. (1974) first suggested that avian proteins evolve more slowly than do those of other organisms. They used the technique of microcomplement fixation and concluded that the ovotransferrins and serum albumins of birds have evolved more slowly than those of mammals, reptiles, or frogs.

The average rate of transferrin evolution in birds was calculated as 1.2 "immunological distance" (I.D.) units per million years, compared with 2.6 I.D. units in mammals and 4.7 in snakes. The authors concluded that the rate of transferrin evolution in mammals is "about twice as great as in birds" and that in snakes it "appears to be nearly 4 times as great as in birds" (p. 253). But the authors did not comment on their evidence showing that snake transferrins apparently evolve 1.8 times as fast as do those of mammals. Thus mammalian transferrins appear to evolve faster than those of birds, but slower than those of snakes.

Prager et al. (1974) used the 27 "orders" of birds recognized by some contemporary avian systematists (e.g., Wetmore, 1960) and an estimate of fossil datings to arrive at an average interordinal divergence time of 100 million years (MY; MYA, million years ago).

It is not easy to refute some aspects of the study by Prager et al. but we do not believe that the fossil datings are accurate nor that the 27 "orders" are equivalent to one another. From our admittedly preliminary and incomplete DNA comparisons it seems clear that some of these "orders" diverged more recently than 85 MY ago. At least one, the "Apterygiformes" of Wetmore (1960), diverged from the "Casuariiformes" not more than 50 MYA (Sibley and Ahlquist, 1981) and few of the living groups diverged

more than 100 MYA (Sibley and Ahlquist, unpublished).

We also doubt that the "orders" of birds, mammals, and reptiles represent equivalent degrees of evolutionary divergence. Instead, we believe that avian orders are excessively "split" and that those of mammals, and perhaps also of reptiles, are overly "lumped." The lack of equivalence between the boundaries of taxonomic categories within and between birds and mammals is demonstrated by the study of Avise et al. (1980a) who defined the problem by stating

that protein evolution in birds appears conservative relative to that of many invertebrate and nonavian vertebrate groups. By conservative we mean only that at equivalent levels of taxonomic recognition many birds appear to exhibit smaller genetic distances at protein-coding loci than of most other kinds of organisms that have been surveyed. The reason for this conservative pattern remains unknown. One possibility is that protein evolution is decelerated in birds; the protein "clock" may tick at a slower pace.

Barrowclough and Corbin (1978:699, table 5) summarized the data from several studies and compared the genetic distances (D) of Nei (1972) for *Drosophila*, fish, salamanders, and mammals with those for birds. For local populations the nonavian average Nei distance (\bar{D}) was 0.037, for birds 0.003; for subspecies the values were 0.199 and 0.008; for species 0.609 and 0.100, and for genera 0.783 and 0.213. Thus, compared with the values for birds, the nonavian distances average nearly 12 times as large for local populations, 25 times for subspecies, six times for species and 3.7 times for genera. If these differences were due only to a slowdown in the rate of avian protein evolution, these ratios should be equal.

Avise et al. (1980a, fig. 1) compared the Nei genetic distances for 27 species of wood warblers (excluding *Icteria*), a thrush (*Catharus*), and a vireo (*Vireo*) with those of 14 species of New World cricetine rodents. For congeneric species

the rodents had an average Nei distance of 0.40, the wood warblers 0.056; for different genera the rodents averaged 1.256, the wood warblers 0.175. In both of these cases the mammalian distances were more than seven times the corresponding values for the birds. *Icteria*, with a D value of 0.48 from other parulines is considered to be an aberrant wood warbler, but the grasshopper mice (*Onychomys*) and the white-footed mice (*Peromyscus*), at a D of 0.56 from one another are considered to be closely related by mammalian systematists. Thus, on the scale used for the cricetines, there would be only two genera of wood warblers for the 28 species examined by Avise et al. (1980a), viz., *Icteria*, plus one other genus for the other 27 species which currently are distributed among 11 genera!

The discrepancy is further demonstrated by the Nei distances among 11 species of *Dendroica* plus those for *Wilsonia*, *Setophaga*, and *Seiurus noveboracensis* which are less (ca. 0.09 maximum) than the distance (0.11) between two closely related species of mice, *Peromyscus maniculatus* and *P. polionotus*. Eleven of the 12 genera of wood warblers examined by Avise et al. (1980a), cluster within a Nei distance of 0.28, which is less than the distance (0.34) between *Peromyscus leucopus* and *P. maniculatus*.

Avise et al. (1980b) have provided another example by comparing the Nei genetic distance values among 13 species of North American sparrows and finches with those among 13 species of sunfishes (Centrarchidae). The 13 avian species are usually placed in eight genera and two families, Fringillidae and Emberizidae. The 123 sunfish species are divided among six genera.

The 13 species of birds have a maximum Nei D value of 0.795 (*Carpodacus: Calcarius*) and among six of the eight genera the maximum D value is 0.327. Species placed in different genera have D distances as low as 0.032 (*Ammodramus sandwichensis: Zonotrichia albicollis*).

The D distances among the sunfishes are much larger. The seven species of *Lepomis* have a maximum D value of ca. 0.70 and the greatest distance between two of the sunfishes is $D = \text{ca. } 1.7$. The smallest D value among the sunfishes is ca. 0.16, between *Lepomis marginatus* and *L. megalotis*. The six genera are well separated from one another and all inter-generic D values are 0.7 or larger.

These examples illustrate the nature of the evidence. If it is assumed that avian taxonomic categories are equivalent to those of nonavian taxa, it does indeed appear that avian proteins diverge more slowly than do those of other animals. But if this assumption is wrong, the apparent slowdown in the rates of change in avian proteins may be an artifact resulting from the different taxonomic evaluations applied to birds which are the result of certain aspects of their biology in which they differ from many other animals.

Birds depend primarily, perhaps entirely, upon vision and hearing to identify conspecifics and to determine their sex. As a result, they have evolved plumage colors and structures, behavior patterns, and vocalizations which function as species-specific and sexual-recognition signals. Conversely, most mammals, salamanders, and invertebrates probably utilize the chemical senses, especially olfaction, for the same purposes. Odors are known to influence reproductive activities in mammals (Bronson, 1974; Stoddart, 1980), and laboratory mice (*Mus musculus*) can distinguish between the odors of conspecific individuals belonging to different histocompatibility groups (Yamazaki et al., 1976, 1979).

Because humans, like birds, are visual-auditory animals, we are able to detect the actual signal characters used by birds for species and sexual recognition. To our eyes and ears the species of birds appear distinct, but we often erect genera based upon the secondary sexual characters of males, especially in those groups in which sexual dimorphism is pronounced. Sibley (1957) discussed this problem,

cited examples from several groups of birds, and concluded that excessive generic splitting by avian taxonomists "is due to erroneous human evaluation of the taxonomic value of the signal characters."

Some diurnal mammals use visual signals and have evolved visible species specific external characters, but most small mammals are nocturnal and even distantly related species and genera tend to look much alike to our eyes. The New World cricetine rodents (Avisé et al., 1980a), although differing widely among themselves on the Nei genetic distance scale (up to $D = 1.8$), are similar in color and general appearance. We perceive them as similar in external morphology and emphasize their similarities by placing them in the same subfamily and in large genera composed of genetically diverse species. Birds are certainly too finely "split" at the generic and familial levels, but small nocturnal mammals may be too "lumped" at these levels.

Some ornithologists have long been aware of these problems which exist even within the Class Aves in which there is a lack of equivalence between passerines and nonpasserines in the taxonomic ranking of supraspecific categories. Sclater (1880:345-6) noted that "the Oscines are all very closely related to one another, and, in reality, form little more than one group, equivalent to other so-called families of birds." Similarly, Gadow (1891:252) suggested that "strictly speaking, all of the Oscines together are of the rank of one family only." Lucas (1894) also emphasized that the passerines have usually been split into too many families, and Fürbringer (1888) recognized only two families of passerines. However, Sharpe et al. (1877-90) used 29 families for the oscines (including Menuridae and Atrichornithidae) and more recent classifications divide the same group into 51 (Stresemann, 1934), 52 (Mayr and Amadon, 1951), or 72 families (Wetmore, 1960). From our preliminary DNA hybridization data we suspect that the oscines (Passeres) are composed of between 10

and 20 clusters that may be approximately equivalent to most of the families of nonpasserines.

The range of opinion about the classification of the Passeres is exemplified by the cluster of taxa known as the "New World nine-primaried oscines." Mayr and Amadon (1951) divided them into five families with seven subfamilies, Wetmore (1960) into eight families, and Wolters (1980) used 12 families and 11 subfamilies. We have proposed that the same groups should be included in a single family (Fringillidae) with two (or three) subfamilies, and eight tribes (Sibley, 1970:99; Sibley and Ahlquist, in press, a, e, f). Sibley (1970:100) suggested that this "should be accompanied by a correlated reduction in the number of genera to be recognized." When Martin and Selander (1975), Martin (1980), and Smith and Zimmerman (1976) found biochemical evidence of close relationships they recommended that certain passerine genera should be merged.

The number of orders into which birds have been divided has also varied widely. Huxley (1867) used only two orders, four suborders, and 24 "groups" the latter apparently equivalent to superfamilies. Sclater (1880) made 26 orders for living birds but Fürbringer (1888) used only seven orders, 21 suborders, 39 "gens," and 76 families, while Seebohm (1890) divided the birds into six subclasses, 14 orders, and 36 suborders.

Among the current classifications, Mayr and Amadon (1951) used 28 orders and Wetmore (1960) used 27, but Wolters (1975:4) divided the living birds into 49 orders. Again, from our preliminary DNA hybridization data, we suspect that living birds can be divided into approximately 20 groups that will merit ordinal rank.

The discrepancy between avian and mammalian orders was apparent to Romer (1962:67) who suggested that "apart from the ratites, most birds . . . are rather uniform in basic anatomic features, with differences between orders no greater than those which distinguish the smaller groups, termed families, among mammals." This

could also mean that the mammalian orders are overly large.

If the number of avian genera is reduced in proportion to the reduction in other categories the discrepancy between avian and mammalian taxa will also be reduced. Bock and Farrand (1980) suggested that the ca. 2945 genera of birds currently recognized could be reduced to ca. 1000. They note that "avian genera are too finely divided and that the genus . . . has limited meaning in avian classification."

Although birds are apparently too finely divided at the generic, familial, and ordinal levels, there is no reason to believe that they are equally oversplit at the species level. In fact, the human perception of avian species is probably more nearly correct than is our perception of species in many other groups of animals. If this is true we should expect to discover cryptic species in some groups whose true distinctiveness can be detected only by comparisons of their proteins, their DNAs, or their actual species recognition signals—for example, odors or pheromones. This expectation has been realized in a few cases as follows.

In an electrophoretic study of 22 protein loci Patton et al. (1976), found that the Heermann Kangaroo Rat (*Dipodomys heermanni*) of southern Oregon and California is actually composed of two well-separated species which had been considered conspecific although one has five toes on the hind feet, the other only four. The two species also differ in the diploid number of chromosomes. Similarly, Highton (1979) discovered a cryptic species of lungless salamander, *Plethodon websteri*, which is morphologically indistinguishable from *P. dorsalis*, but electrophoretically different at 80% of 26 genetic loci. The two species are sympatric at one locality in Alabama.

Manwell and Baker (1963) discovered a sibling species of sea cucumber (Echinodermata:Holothuroidea) when they found two distinct electrophoretic patterns in a population supposedly representing a single species. After the two species were characterized electrophoretically the authors found correlated morphological differences

which had been attributed to individual variation.

In birds there are valid species that are difficult to distinguish visually but whose vocalizations are species specific. Examples include the tyrannid genera *Empidonax* (Stein, 1963; Johnson, 1963), *Myiarchus* (Lanyon, 1978), and *Contopus* (Rising and Schueler 1980). Conversely, some avian subspecies are so different in external morphological characters that they were long considered to be separate species—for example, the eastern, western, and southwestern races of the Common Flicker (*Colaptes auratus*) (Short, 1965), the eastern and western races of the Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Sibley, 1950; Sibley and West, 1959), and the eastern and western races of the Yellow-rumped Warbler (*Dendroica coronata*) (Hubbard, 1969; Barrowclough, 1980).

It is also clear that closely related species of birds can exist in sympatry without hybridizing. The visible and audible species-specific recognition signals of birds are detectable at a considerable distance and function as premating isolating mechanisms which prevent pair formation. Evidence for this comes from the occasional hybrids between congeners that are widely sympatric but which hybridize only where one of them is uncommon and, therefore, the choice of mates is limited. Examples include the woodpeckers *Picoides pubescens* and *P. nuttallii* (Short, 1969) and the bulbuls *Pycnonotus cafer* and *P. leucogenys* (Sibley and Short, 1959).

However, even if hybrids do occur between closely related species of small mammals, salamanders, or other groups of visibly similar species, they would be difficult to detect by the examination of standard museum specimens. The detection of avian hybrids is much easier because the plumage characters of most closely related species are visibly different and the hybrids are distinctive.

There are probably other factors pertinent to this problem but we believe that the evidence for an alternative explanation for

the suggested slowdown in the evolution of avian proteins is sufficient to render it doubtful. We suggest that the alleged slowdown is primarily the result of the limitations of human perception, not of some unknown difference between the genomes of birds and other animals.

The problem of the equivalence of taxonomic categories is not confined to the genera and families of vertebrates. Van Valen (1973) questioned the equivalence of the categories in different phyla and it seems clear that the nonequivalence we have noted among birds, fishes, and mammals begins with the lack of equivalence between the groups usually designated as "Classes" in the vertebrates. These are the Agnatha (jawless fishes), Placodermi (jawed, armored fishes), Chondrichthyes (sharks, rays), Osteichthyes (bony fishes), Amphibia, Reptilia, Mammalia, and Aves. These groups are traditionally treated as categorical equivalents, but the Agnatha appear in the fossil record as the jawless ostracoderms in the Ordovician (ca. 450 MYA), the placoderms, Chondrichthyes and Osteichthyes in the late Silurian or early Devonian (ca. 400 MYA), the Amphibia in the late Devonian (ca. 350 MYA), the Reptilia in the Carboniferous (ca. 300 MYA), the Mammalia in the Triassic (ca. 195 MYA), and the Aves in the Jurassic (ca. 130 MYA). The oldest "Class" is nearly three times as old as the youngest. Furthermore, it is apparent that the later groups diverged from the earlier ones and we therefore have Classes evolving from Classes, a logical *non sequitur*. Each so-called Class of vertebrates is subdivided into orders, families, etc., using intraclass characters and the inevitable result is categorical nonequivalence throughout the system.

The idea that categorical levels might be based upon times of divergence was rejected by Simpson (1937) and Mayr (1969:72,230) because it seems apparent that we perceive morphological change as proceeding at many different rates, and there is no way known to quantify the degrees of difference among morphological characters to reflect degrees of evolutionary

divergence. However, Simpson (1944:3) stated that "Rate of evolution might most desirably be defined as amount of genetic change in a population per year, century, or other unit of absolute time." But, in 1944, there was no way to measure such a rate of genetic change so Simpson defined the rate of evolution as the "amount of morphological change relative to a standard" and assumed that phenotypic evolution implies genetic change and that rates of morphological evolution "are similar to, although not identical with, rates of genetic modification." This assumption has been implicit (and often explicit) in all morphologically-based classifications of recent years. Unfortunately, it is not true (e.g., Wilson, 1976).

Hennig (1966) has been the principal, if not the only, proponent of the age of origin as the basis for the absolute ranking of taxa. He considered the equivalence of ranking to be a serious and important problem, the lack of which is an enormous burden upon systematics that prevents the development of a consistent and maximally useful classification. Hennig (1966:84, 146, 156, 160) recognized the limitations of morphology as the basis for determining the absolute rank order of taxonomic groups; so he proposed (pp. 180–182) that the relative rank be determined from morphology and that, where possible, fossil datings and other evidence be used to establish reference points in the system. He suggested that "there is no single method with which the age of origin can be determined accurately" and that only minimal and maximal limits can be recognized.

As a compromise, Hennig (p. 191) suggested that the present absolute ranking be retained in most groups and that a "conversion chart" be developed to show the equivalent categories in different groups.

Hennig's reason for favoring such a compromise identifies one source of the problem, and what will surely be a barrier to the general acceptance of a time-based ranking of categories. He wrote (p. 191),

... taxonomists are essentially specialists — entomologists, arachnologists, ornithologists, etc. — who ... usually work only in certain sections of these extensive areas. All these specialists work as if only their group of animals existed. Consequently each specialist can erect a consistent phylogenetic system for his group without any necessity for correspondence on the basis of equivalent age between the absolute rank order of his categories and the absolute rank order of other groups of animals. Presumably even the most convincingly presented objective reasons will not bring these specialists to the point of giving up life-long habits and speaking of classes and orders where they are accustomed to speaking of families and vice versa.

We agree with Hennig that the absolute ranking of taxonomic categories should be based upon the age of origin, and that sister groups should be of equivalent rank. But our reasons for supporting this position are based upon evidence from DNA comparisons which indicate that the *average* rate of DNA evolution (i.e., nucleotide substitution) is the same in all lineages. This *uniform average rate* of genetic change meets Simpson's (1944:3) criterion for the most desirable definition of the rate of evolution and is concordant with Hennig's arguments in favor of a time-based ranking of taxa.

We have presented the arguments and evidence for the uniform average rate elsewhere (Sibley and Ahlquist, 1981; in press,^a; Sibley, Williams, and Ahlquist, in press). The essential points are that DNA hybridization measures the net divergence between the homologous nucleotide sequences of different taxa and that the uniform average rate of change is a statistical result of the large number of nucleotides in the eukaryotic genome, e.g., ca. 2×10^9 in mammals and birds. Each nucleotide evolves at its own rate, and different sequences evolve at different rates at different times, but when *averaged* over the genome and over time, the uniform average rate is the inevitable result because there are upper and lower bounds to the rates

and the frequency distribution of rates is narrow relative to the number of nucleotides. Thus the rates are not constant, but the *average rates in all lineages are uniform*.

This means that the DNA hybridization data provide the relative time of divergence for any two taxa that are compared. When the DNA values are calibrated against geological or fossil dates the DNA data provide the absolute times of branching and may, therefore, be used to develop a time-based absolute ranking of taxa which is equivalent to genetic divergence. Because of technical limitations the DNA hybridization data can be used only for taxa that diverged during approximately the past 150 MY. However, there are other techniques that can extend the time to the earliest periods of life on Earth. For example, the sequences of the 16S ribosomal RNAs have been used to determine phylogenetic relationships among bacteria, including divergences that occurred as much as three billion years ago (Fox, et al., 1980; Woese, 1981).

We therefore propose that the major, and especially the older, dichotomies be dated by the best available fossil and/or nucleic acid sequence evidence and that DNA hybridization data be used to develop a genetic divergence-based, and hence time-based, system of taxonomic categories representing the dichotomies of the last 150 MY. This can largely solve the rank equivalence problem although, as Hennig so pessimistically predicted, it may take a generation or two of systematists to win acceptance.

Acknowledgments

For assistance in the laboratory we thank C. Barkan, M. Pitcher, N. Snow, and F.C. Sibley. The computer program was written by T.F. Smith. For advice we are indebted to R.J. Britten, D.E. Kohne, R. Holmquist, G.F. Shields, W.F. Thompson, H.E. Burr, and W.M. Fitch.

For assistance in the field we thank F.C. Sibley, J. Spendelov, J. O'Neill, R. Semba, J. duPont, and N. and E. Wheelwright.

The laboratory work was supported by Yale University and the National Science Foundation (DEB-77-02594 and DEB-79-26746).

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