

**WHERE DO THE LOONS GO?
A FIELD GUIDE TO DNA CLASSIFICATION
OF NORTH AMERICAN BIRDS**

by John C. Kricher

You probably know the order pretty much by heart, starting with Common Loon: loons first, then grebes, continuing through the waterbirds with raptors and gallinaeous birds placed between herons and shorebirds; then gulls and terns, alcids, owls, doves, continuing through woodpeckers, jays and crows, chickadees, wrens . . . well, you know. Finally you get past the vireos, wood-warblers, and blackbirds to the finches, sparrows, longspurs, and Snow Bunting—and the end of the field guide. Those of us who cut our birding teeth on the various editions of the Peterson or Pough guides soon learned the accepted taxonomic arrangement of bird families, an arrangement decided upon by the American Ornithologists' Union (AOU) based on presumed evolutionary relationships (phylogeny), as largely determined by careful study of anatomy. The AOU periodically publishes its *Check-list of North American Birds*, where avian taxonomy is updated according to the most recent studies: some species are split, others lumped, new records accepted or rejected, and any changes in taxonomic sequence incorporated. In 1983 the National Geographic Society, reflecting changes announced in the Sixth Edition of the AOU Check-list (AOU 1983), tossed birders a bit of a knuckleball, so to speak. The then new NGS field guide ended with Evening Grosbeak, not Snow Bunting, the traditional finale of other field guides. Finches and sparrows were split, each species placed into one of two big families, either the Emberizidae (wood-warblers, bananaquits, tanagers, cardinals, grosbeaks and allies, emberizine sparrows and towhees, and blackbirds and allies) or Fringillidae (fringilline and cardueline finches and Hawaiian honeycreepers). Suddenly it became just a bit more difficult to quickly locate certain species. Are Northern Cardinals and Rose-breasted Grosbeaks emberizids or fringillids? (Emberizids) What about Pine and Evening grosbeaks? (Fringillids) Blackbirds and orioles now followed towhees and sparrows but preceded crossbills and goldfinches. True, many species were not where they used to be, but at least the loons still came first and the grebes were in their accustomed place, next. The old order had been revised but not revolutionized.

Molecular Taxonomy

Today, a new, much more radical look is suggested, an arrangement based entirely on biochemistry. Unlike previous taxonomic sequences, this one does not compare feathers or bones, but molecules of DNA. Genes, the stuff of heredity, are all made of a long-coiled, information-packed molecule called

deoxyribonucleic acid (DNA), and genes make the bird. The components of DNA, called nucleotides, like letters in a sentence, are arranged in a very precise order, an order that determines the shape, size, physiology, and vast majority of other measurable attributes of everything from kiwis to kiwi fruits. Ultimately a bird, any bird, a cat, any cat, a tree, any tree, is what it is essentially because of the highly specific informational content of its DNA. DNA is the recipe—the organism is the cake. If the DNA codes for feathers, it's making a bird.

Your DNA is, of course, most similar to that of other human beings. That's why you resemble your neighbors more closely than you resemble their Labrador retriever. Outside of human comparisons, your DNA is most similar, incredibly similar, in fact, to chimpanzee DNA. To continue, your DNA is more similar to that of a dog (Lab, poodle, or otherwise) than it is to that of an iguana. And, as you might by now have guessed, it's more similar to an iguana than it is to a pine tree or mushroom. By examining similarities among DNA from various species, you are making comparisons that allow you to look indirectly into the past, into the biological archives, revealing the pattern of evolution from a common ancestor, the very essence of Darwin's evolutionary paradigm, "descent with modification." Changes in DNA with time *are* evolution. The pattern of DNA differences within a group should, in fact, directly reveal the evolutionary relationships among each member, revealing genealogy on its grandest scale.

DNA/DNA Hybridization

In recent years, as knowledge and techniques of molecular biology have burgeoned, it has become possible to extract DNA from its well-protected haven within the nucleus of the cell and in the laboratory hybridize DNA taken from different organisms. This is because DNA is double stranded, the famous "double helix," first described over four decades ago by Francis Crick and James Watson. The two strands of the double helix, isolated in the laboratory, can be heated and made to separate, and one strand can then be combined with that from a different species. Rest easy, nothing comes of the hybrids. You need not fear questions such as "what do you get when you cross a carrot with a sturgeon?" Perhaps caviar with a high content of beta carotene? No, no, the hybridized molecules never leave the test tube. In fact, the more dissimilar the DNA of two different organisms is, the less it is prone to hybridize, and therein lies the key. The degree of fidelity with which separate strands of DNA from different organisms reunite, hybridize in other words, is dependent on how similar they are to one another, a similarity essentially resulting from evolutionary history. If two species separated from their common ancestor eons ago, their respective complements of DNA would have traveled separate paths through time for many millions of generations—the DNA would have become quite distinct between them. Their molecules would hybridize weakly. However,

if the two species shared a very recent common ancestor, as in all likelihood have humans and chimps, then the two DNAs would hybridize tightly, being nearly identical to one another. How do we know how tightly the strands hybridize, and thus how similar they are to one another? Heat breaks the relatively weak molecular bonds that hold the double helix together. The more heat that must be used to reparate hybrid strands, the more bonds there are between them and thus the more similar the two strands are to one another. Separation temperature can thus be calibrated with the degree of DNA similarity between the hybrid strands.

Convergent Evolution

You might at this point be tempted to ask, but why is DNA better for establishing evolutionary histories than anatomy or physiology, or any of the other numerous attributes of organisms? Biologists have long known about a phenomenon known as convergent evolution, when two distantly related organisms converge in appearance, making them look much more closely related than they really are. A classic example of convergent evolution is the anatomical similarity between placental animals and their marsupial equivalents in Australia. For example, an Australian sugar glider looks strikingly like a flying squirrel, although these two organisms are only very distantly related genetically. Convergent evolution is among the most persuasive evidence for the reality of natural selection as a driving force in evolution. Two genetically distinct organisms can evolve similar anatomies in response to similar selection pressures imposed by their respective environments. Convergent evolution occurs in plants as well as in animals. New World cacti and Old World euphorbias are remarkably similar in appearance, although not at all close genetically. The reality of convergent evolution makes anatomy somewhat problematic when used to determine evolutionary history. How does one know whether two species are similar because they share a very recent genetic history, or because they have converged (and thus may be quite genetically distinct)?

Consider that the DNA directs the making of bones, muscles, nerves, and brain. DNA makes the feathers, feathers do not make the DNA. DNA is thus the ultimate currency of evolution, quite appropriately termed the "master molecule." Now it is quite possible that two different arrays of genes can independently direct the construction of similar looking organisms, but the sets of genes themselves will remain different. Thus, by looking directly at the DNA, the possible confusion caused by convergent evolution is greatly reduced.

For example, looking at the genes through DNA/DNA hybridization indicates that there is a very tight evolutionary relationship between New World vultures and storks, a relationship so close as to justify lumping both groups in the same family, the Ciconiidae. The close superficial resemblance between our vultures and those from Africa and other parts of the Old World is a case of

convergent evolution; the two distantly related groups look very similar because they have evolved nearly the same adaptations in response to similar selection pressures imposed by their respective environments. Different sets of genes have built similar organisms, but the similarity is only skin deep. Inside the nuclei of the cells, the genes tell of different origins.

Another point, also important, has to do with sample size provided by using DNA rather than anatomy. Professors are only too familiar with plagiarism, the regrettable decision by a student to merely copy someone else's work rather than to do one's own work. How is plagiarism established? When hundreds, and usually thousands of letters are arranged in an order (as sentences and paragraphs) that essentially duplicates another already existing sequence. What is the probability that two papers of 500-1000 words read almost or exactly the same due to chance alone? Remote, to say the least. A student turning in such a paper is in all probability guilty of having plagiarized someone's work. Now consider DNA. What is the probability that two organisms will share the vast majority of millions of letters (nucleotides) arranged in nearly exactly the same order? When two DNA molecules from different organisms are hybridized, and they hybridize tightly, that is exactly what happens. Such a fidelity cannot be due merely to chance, but much more likely indicates shared evolutionary history. And bear in mind that evolutionary histories based on DNA are relying directly on many millions of bits of information. If you want to do a thorough anatomical analysis of a bird, chances are good that you might measure over a thousand characteristics, but you'll not approach a million. DNA analysis therefore represents a far greater sample size of information, thus strengthening conclusions drawn from DNA-based studies.

The SAM System

Charles Sibley, John Ahlquist, and Burt L. Monroe, Jr., took on the Herculean task of examining the roughly 9000 species of the world's birds on the basis of DNA similarities, employing as well as pioneering the technique

Classification Nomenclature (AOU Check-list 1983)

Blackburnian Warbler

Kingdom	Animalia
Phylum	Chordata
Class	Aves
Order	Passeriformes
Family	Emberizidae
Genus	<i>Dendroica</i>
Species	<i>fusca</i>

they called DNA/DNA hybridization (Sibley and Monroe 1990, 1993; Monroe and Sibley 1993). The results of their labors is a taxonomy that now bears the nickname SAM (for Sibley, Ahlquist, and Monroe). Thousands of hybrid DNA molecules were generated in their laboratory, and their's and other labs continue working today. Their results have revealed many examples of convergent evolution as well as cases where species that look quite distinct from one another are genetically very close (witness the human/chimp example). The disquieting conclusion of the SAM work is that the genes are quite often *not* a direct reflection of appearances. Not only that, but the degree of similarity and difference between species can be calibrated (using the fossil record) on a time scale, a kind of evolutionary clock. Doing so reveals approximately when two groups split, diverging from their common ancestor. Using SAM technology, it is possible to construct an evolutionary (phylogenetic) tree, tracing ancestry based entirely on similarities among DNA.

The New Look

Because the pattern of the genes is not always the same as the pattern suggested by bones and feathers, the classification of the world's birds changes, often dramatically, sometimes radically, when DNA similarity is the determining factor. Loons it seems, are not the most evolutionarily ancient birds on the North American list. They no longer come first. Would you believe Plain Chachalaca, followed by Chukar, then Common Pheasant (Ring-necked subspecies), then Spruce Grouse? Indeed, the new world order of DNA-based bird taxonomy makes the break-up and subsequent realignment of the Soviet Union look somewhat lame by comparison. For only those orders found in North America (including introduced species), Table 1 compares the proposed list (from Monroe and Sibley 1993) versus the current AOU Check-list (1983) order. The list shown in Table 1 is not a cladogram. It is meant only to show the sequence from most anciently evolved to most recently evolved, not to imply, for instance, that ducks gave rise to woodpeckers and that hummingbirds gave rise to barn owls. The actual tracing of lineages is a complex branching diagram, not a simple linear ordering.

Given the immensity of the Passeriformes, you might like to see a DNA-based breakdown of the revised order of passerine families. Table 2 shows the revised order compared with the current AOU Check-list (1983) order. The last bird on the North American list, as well as the world list, is Bobolink. Please keep in mind that this classification is not meant to suggest that the Bobolink is the most recently evolved of the world's bird species, but that it is a member of the most recently evolved families and that, within that family, its DNA suggests a very recent origin. Nonetheless, there are many other species of birds more recently evolved than Bobolinks but that are members of older families. Thus their DNA profile puts them in groups that appear earlier in this linear ordering of families.

Table 1
Comparison of Sequence of Orders
AOU Check-list (1983) Versus DNA/DNA Hybridization

<u>AOU Check-list</u>	<u>DNA/DNA Hybridization</u>
Gaviiformes: loons	Craciformes: chachalacas, guans, curassows
Podicipediformes: grebes	Galliformes: pheasants, turkeys, grouse, quails
Procellariiformes: albatrosses, shearwaters, petrels, storm-petrels	Anseriformes: swans, geese, and ducks
Pelecaniformes: tropicbirds, boobies, gannets, pelicans, cormorants, frigatebirds	Piciformes: woodpeckers
Ciconiiformes: bitterns, herons, ibises, storks	Trogoniformes: trogons
Phoenicopteriformes: flamingos	Coraciiformes: kingfishers
Anseriformes: whistling-ducks, swans, geese, ducks	Cuculiformes: cuckoos, anis, roadrunners
Falconiformes: New World vultures, ospreys, hawks, caracaras, falcons	Psittaciformes: parrots
Galliformes: chachalacas, grouse, quail, turkeys	Apodiformes: swifts
Gruiformes: cranes, rails	Trochiliformes: hummingbirds
Charadriiformes: plovers, oystercatchers, stilts, avocets, sandpipers, phalaropes, jaegers, skuas, gulls, terns, skimmers, auks	Strigiformes: barn owls, typical owls, nightjars

AOU Check-list

Columbiformes: pigeons, doves

Psittaciformes: parrots

Cuculiformes: cuckoos and anis

Strigiformes: barn owls, typical
owls

Caprimulgiformes: goatsuckers

Apodiformes: swifts, hummingbirds

Trogoniformes: trogons

Coraciiformes: kingfishers

Piciformes: woodpeckers and allies

Passeriformes: flycatchers, larks,
swallows, jays, magpies, crows,
chickadees, titmice, nuthatches,
creepers, wrens, dippers, kinglets,
mimic thrushes, thrushes, pipits,
waxwings, shrikes, starlings,
vireos, wood-warblers, tanagers,
grosbeaks, buntings, towhees,
sparrows, blackbirds, finches,
weaver finches

DNA/DNA Hybridization

Columbiformes: pigeons and doves

Gruiformes: cranes and rails

Ciconiiformes: shorebirds, gulls,
terns, alcids, raptors, grebes,
tropicbirds, sulids, anhinga,
cormorants, herons, egrets,
bitterns, flamingos, ibises,
spoonbill, pelicans, New World
vultures, storks, frigatebirds,
penguins, LOONs, petrels,
shearwaters, albatrosses, storm-
petrels

Passeriformes: tyrant flycatchers
and all other passerines

Table 2
Comparison of Sequence of Passeriformes Families
AOU Check-list (1983) Versus DNA/DNA Hybridization

<u>AOU Check-list</u>	<u>DNA/DNA Hybridization</u>
Tyrannidae: tyrant flycatchers	Tyrannidae: tyrant flycatchers
Alaudidae: larks	Laniidae: shrikes
Hirundinidae: swallows	Vireonidae: vireos
Corvidae: jays, crows	Corvidae: crows and jays
Paridae: titmice	Bombycillidae: waxwings
Aegithalidae: Bushtit	Cinclidae: dippers
Sittidae: nuthatches	Muscicapidae: thrushes
Certhiidae: tree creepers	Sturnidae: starlings, mynas, and mimic thrushes
Pycnonotidae: bulbuls	Sittidae: nuthatches
Troglodytidae: wrens	Certhiidae: tree creepers, wrens, and gnatcatchers
Cinclidae: dippers	Aegithalidae: Bushtit
Muscicapidae: kinglets, gnatcatchers, Old World flycatchers, thrushes, solitaires	Hirundinidae: martins and swallows
Mimidae: mimic thrushes	Regulidae: kinglets
Motaciliidae: pipits	Pycnonotidae: bulbuls
Bombycillidae: waxwings	Sylviidae: Old World warblers, Wrentit
Ptilogonatidae: silky-flycatchers	Alaudidae: larks
Laniidae: shrikes	Passeridae: weaver finches, pipits
Sturnidae: starlings	

AOU Check-list

Vireonidae: vireos

Emberizidae: wood-warblers,
tanagers, cardinals and allies,
blackbirds and allies, Emberizines
(sparrows, towhees)

Fringillidae: Cardueline finches
(i.e., House Finch, crossbills,
goldfinches)

Passeridae: House Sparrow

DNA/DNA Hybridization

Fringillidae: Olive Warbler,
siskins, goldfinches, redpolls,
Evening Grosbeak, Snow Bunting,
sparrows, juncos, towhees, wood-
warblers, tanagers, Dickcissel,
other grosbeaks (i.e., Northern
Cardinal, Rose-breasted),
blackbirds, orioles

As I stated earlier, the revised classification of birds is meant to reflect evolutionary relationships based solely on DNA compatibilities. Anatomy, plumage, behavior, or any other characteristic does not enter into the determination. Further, the classification is meant to suggest that the most ancient groups of birds in North America are the chachalacas, the gallinaceous birds, and the waterfowl. Loons? As you see, they are lumped in a huge and diverse order, the Ciconiiformes, which worldwide includes 255 genera and 1022 species, encompassing such seemingly disparate groups as penguins, hawks, storm-petrels, and cormorants. Grebes are there too, but well separated from loons. The genes are saying that the Horned Grebe is more genetically like a Peregrine than a Red-throated Loon, even though grebes look much more like loons than raptors.

Some of the changes in classification seem unsurprising, at least to me. Yes, a Great Horned Owl looks only remotely like a Whip-poor-will. However, if you travel to other parts of the planet and have occasion to gaze upon the likes of potoos, frogmouths, or owlet-nightjars, the line between the strigids and the caprimulgids seems to blur. The DNA agrees: caprimulgids are lumped with the owls. The night birds are now placed all together in one order, the Strigiformes.

Among other surprising realignments is the inclusion of mimic thrushes in the family Sturnidae, the starlings and mynas. It is true that the chunky,

loathsome creatures that nightly roost in our cities (I mean, of course, the European Starlings) bear faint anatomical resemblance to the likes of a sleek Brown Thrasher or Northern Mockingbird. But, isn't it more than a little interesting that Old World starlings and mynas are known for their extraordinary abilities to mimic other birds? In the case of starlings and mimic thrushes the genes made the voice boxes similar and the bodies different.

In the Sixth Edition of the AOU Check-list the large family Muscicapidae includes the Old World warblers (including the ones you trek to Alaska, especially Attu, to see), the kinglets, the gnatcatchers, the Old World flycatchers (more Attu species here), all the thrushes, and accentors. The genes say otherwise. According to DNA similarities, Muscicapidae now includes only thrushes and Old World flycatchers. You just learned where the mimic thrushes have gone. The kinglets are removed from Muscicapidae, now placed in their own distinct family, Regulidae, well separated from the gnatcatchers that have been lumped in the family Certhiidae, along with wrens and tree-creepers. The Old World warblers are now within the family Sylviidae, a large group of mostly Old World species that includes such groups as the babblers and allies—and the Wrentit. Long thought to be a member of the Muscicapidae, the Wrentit is genetically closer to babblers (although still unique), and is placed in its own tribe, the Chamaeini. (A tribe is a subdivision within the level of subfamily that shares all of the characteristics of the subfamily but is nonetheless unique in some important ways. Creating tribes adds a finer degree of separation among very closely related subfamilies.)

Yet another surprise is the genetic proximity between the weaver finches, accentors, wagtails, and pipits, now lumped together in the family Passeridae, a huge grouping that includes the colorful Old World estrildine finches (many of which are common cage birds) and exotic whydahs and paradise-whydahs. It is a stretch to believe that the elegant, tail-bobbing American Pipit is a close cousin of the all too common House Sparrow, but their respective genes seem to so indicate.

Most recently, in what can only be described as an immense burst of evolutionary creativity, a cornucopia of (mostly) recently evolved species are grouped within the family Fringillidae. The split into the Emberizidae and the Fringillidae has been abolished. The two families have been lumped into a single immense family totaling 241 genera and 995 species, most of them found in the New World, mostly in the subtropics and tropics.

To try to make sense of this grouping, it is necessary to look at the level of subfamily, and even that is complex. But it begins with but a single species in a unique subfamily, the Peucedraminae. It is the Olive Warbler, which is not a true wood-warbler, at least not according to its DNA. The Olive Warbler, a curious species of the southeastern Arizona mountain pine forest, a bird that certainly looks and acts like a wood-warbler, is most closely related to, of all

things, the Chaffinch, an abundant and widely distributed species in Europe, Asia, and parts of Africa. The Chaffinch is in the major subfamily Fringillidae, including 170 species of largely Old World birds. Its nearest North American relatives are siskins and goldfinches, followed by the rosy-finches, the *Carpodacus* finches (Purple Finch and allies), the crossbills, and the Pine and Evening grosbeaks. And there is yet one other group in this subfamily, the Hawaiian honeycreepers (now more properly termed the Hawaiian finches [tribe Drepanidini]), a group of thirty species (of which eight are extinct) all endemic to the Hawaiian archipelago. The Hawaiian finches represent a considerably more dramatic divergence from their common ancestor (quite possibly a nomadic species such as Red Crossbill) than the thirteen species of Darwin's finches from the Galapagos Islands.

The family Emberizidae is now the subfamily Emberizinae, boasting a total of 201 genera and 824 species. Within this massive subfamily, all the longspurs (and Snow Bunting), juncos, towhees, and New World sparrows are together in the tribe Emberizini, numbering 157 species. Next is the tribe Parulini, the 115 species of wood-warblers, followed by the tribe Thraupini, the 413 species of tanagers and allies. This diverse tribe includes the (mostly subtropical and tropical) New World seedeaters, grassquits, seed-finches, and Darwin's finches. According to DNA analysis, the nearest living relative of the Darwin's finches is the St. Lucia Black Finch, although many ornithologists still believe the Blue-black Grassquit is the more likely ancestor. The Emberizinae continue with the tribe Cardinalini, forty-two species that include the Dickcissel, Rose-breasted and Black-headed grosbeaks, Northern Cardinal, Pyrrhuloxia, and the *Passerina* buntings.

The final Emberizid tribe is the Icterini, a group of ninety-seven species that encompasses all the orioles and allies, the meadowlarks, the blackbirds and grackles, the cowbirds, and the Bobolink, the last species of the 9702 included on the DNA-based world list (Monroe and Sibley 1993).

What Does It All Mean?

What, if any, conclusions can be drawn from the new ornithological classification based on DNA? First, if you are a betting person, put some money into backing a new field guide that uses this sequence rather than the previous anatomically based taxonomy. You could afford to go on more birding trips, for instance. More seriously, DNA analysis has challenged an array of standard practices and assumptions among ornithologists. Those who rely heavily on comparative anatomy, indeed a discipline that forms one of the traditional bastions of support for evolution, have to be wary of both "false positives" and "false negatives." Birds that look anatomically alike (such as Olive Warbler compared with various wood-warblers) may be only distantly related. Birds that look quite different (European Starling compared with Gray Catbird) may be

genetically close, sharing a much more recent common ancestor than their different anatomies would suggest. Of course, in many species the DNA and anatomical studies do correlate closely. Anatomists have long known that New World vultures and storks both share some compelling anatomical and behavioral similarities (such as defecating on their legs to facilitate heat loss in hot climates) that have suggested to some evolutionists that they share a close genetic kinship. DNA analysis now confirms that long held speculation. All of the *Empidonax* flycatchers are very much alike with regard to anatomy and plumage, and their DNA also suggests a very recent common ancestry.

As with any relatively new technology, DNA/DNA hybridization has its critics and skeptics. Many ornithologists are still reserving judgment regarding the accuracy of the technique. Some argue, for instance, that the assumptions underlying the "molecular clock," the rate and constancy of DNA mutation, are far from proven. Although it may be fair to characterize the latter part of the twentieth century as the "age of molecular biology," the genes do not give up their secrets easily, and there is still much to learn about the double helix. It is entirely possible that further work on DNA will necessitate additional revisions in phylogeny, as more is learned.

Nonetheless, DNA analysis has, it is fair to say, done more than merely fine tune what anatomical and other studies have already determined. It has probably raised as many interesting evolutionary and biogeographical questions as it has answered. Many ornithologists remain somewhat if not outright skeptical about some of the ordering of species as well as about the overall accuracy of DNA hybridization techniques and assumptions. Ferment now fills taxonomy, a discipline once considered about as dull as any, but one that is now at the center of both a new and challenging methodology as well as the newly emerging interest and concern for global biodiversity. Ornithologists await the publication of the Seventh Edition of the AOU Check-list, currently overdue, but soon to be published. Not all of the DNA-based changes will likely be accepted, but the new check-list will no doubt look quite different from its predecessor.

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