A Phylogenomic Study of Birds Reveals Their Evolutionary History

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Deep avian evolutionary relationships have been difficult to resolve as a result of a putative explosive radiation. Our study examined ~32 kilobases of aligned nuclear DNA sequences from 19 independent loci for 169 species, representing all major extant groups, and recovered a robust phylogeny from a genome-wide signal supported by multiple analytical methods. We documented well-supported, previously unrecognized interordinal relationships (such as a sister relationship between passerines and parrots) and corroborated previously contentious groupings (such as flamingos and grebes). Our conclusions challenge current classifications and alter our understanding of trait evolution; for example, some diurnal birds evolved from nocturnal ancestors. Our results provide a valuable resource for phylogenetic and comparative studies in birds.

Although well studied, the evolutionary relationships among major avian groups are contentious (*1*–*6*). Recovering deep evolutionary relationships in birds is difficult, probably reflecting a rapid divergence early in their evolutionary history (*1*–*3*, *7*, *8*) that has resulted in many distinctive, morphologically cohesive groups (e.g., owls, parrots, and doves) with few, if any, extant intermediary forms linking them to other well-defined groups. This extreme radiation also makes it difficult to place fossil taxa, which further contributes to the difficulty in precisely timing avian divergences (*3*, *9*).

Only two nodes at the base of the avian tree are consistently supported by both molecular and morphological phylogenetic studies (*2*–*5*, *10*–*14*). The first divides the Paleognathae (ratites and tinamous) and Neognathae (all other birds), and the second splits the neognaths between the Galloanserae (chickens, ducks, and allies) and Neoaves (other neognaths). Although the Neoaves represents the majority of avian diversity (95% of extant species) and is the focus of most comparative studies, little consensus exists regarding relationships within this clade (*1*–*5*, *8*). The absence of intermediate forms linking well-defined groups, combined with the difficulty of resolving relationships, led to hypotheses that the base of Neoaves represents an unresolved evolutionary radiation (polytomy) (*7*, *8*). Previous efforts to reconstruct these phylogenetic relationships have been limited by taxon sampling, the number of loci, and/or slowly evolving loci with limited power to resolve short internodes [e.g., (*3*, *4*, *10*, *12*, *14*)]. Moreover, conflicting results have been obtained with morphology (*13*, *15*), DNA-DNA hybridization (*6*), whole mitochondrial genomes (*16*–*18*), and different nuclear exon, ribosomal RNA, and intron sequences (*1*, *3*, *4*, *10*, *12*, *14*).

Phylogenomics is useful for resolving difficult phylogenies and for verifying or overturning relationships created on the basis of single genes (*19*–*21*). We collected a large DNA sequence data set to address avian phylogenetic relationships from 171 species representing all but three nonpasserine families, all major passerine clades, and two crocodilian outgroups (*22*). Our alignment of 32 kb represents 19 nuclear loci located on 15 different chromosomes in the chicken genome (*22*), with introns (74%), coding exons (23%), and untranslated regions (UTRs) (3%). Data quality and sequence alignments were assessed before analyses (*22*). We analyzed the data using different optimality criteria and distinct tree-search algorithms (*22*).

Our sampling of many loci allowed us to assess whether relationships were supported by a signal across the genome or were driven by a single locus. We (i) analyzed individual loci, (ii) conducted "gene-jackknifing" (excluding one locus at a time, then analyzing the remaining data) to determine whether conclusions were driven by a single locus, (iii) conducted a partitioned–maximum likelihood (ML) analysis (where each locus had a distinctive set of parameters), and (iv) coded the data as R (purine) or Y (pyrimidine) to avoid conclusions driven by base-compositional biases [e.g., (*16*)].

Analyses of individual loci showed that no single gene was able to recover all nodes identified with the concatenated data (Fig. 1). The low power of individual loci was the most pronounced in short and slowly evolving genes, which generally did not resolve any interordinal relationships (Fig. 1).

Consistent with previous studies, we recovered genome-wide support for basal divergences between Paleognathae and Neognathae and between Galloanserae and Neoaves (Fig. 2) with robust support. The topology at the base of Neoaves, with extremely short internodes, indicated a rapid radiation (Fig. 3) that likely explains conflicts among previous studies. However, we consistently found several, well-supported, deep divisions within Neoaves (highlighted in different colors in Figs. 2 to 4).

Our study (i) revealed robust higher-level groupings within Neoaves, (ii) suggested several previously unrecognized interordinal relationships, (iii) supported previously proposed clades, (iv) reinforced established relationships not consistently recovered in previous studies, and (v) found well-supported groupings at the tips of major clades. The results discussed below focus on groups that are found with multiple analytical methods and partitions and that exhibit strong support (ML bootstrap support ≥ 70%) (*23*).

The largest clade in Neoaves was a well-supported land bird clade (green, node F, Fig. 2) (*3*) that contained the Passeriformes (perching birds, representing more than half of all avian species), which is allied with several morphologically diverse orders. These included Piciformes (woodpeckers and allies), Falconiformes (hawks and falcons), Strigiformes (owls), Coraciiformes (kingfishers, hornbills, rollers, and allies), Psittaciformes (parrots), Coliiformes (mousebirds), and Trogoniformes (trogons). One of the most unexpected findings was the sister relationship between Passeriformes and Psittaciformes (node A, Fig. 2), with Falconidae (falcons) sister to this clade. This relationship varied slightly among analyses and gene-jackknifing (Fig. 1), yet the close relationship between passerines with parrots and/or falcons appeared consistently.

Sister to the land birds is the Charadriiformes (shorebirds, gulls, and alcids; yellow, node G, Fig. 2). This grouping seems to be driven primarily by the β-*fibrinogen* gene (*FGB*), because it was present in analyses of only this gene and disappeared when the gene was removed through jackknifing (Fig. 1). Regardless of the exact placement of the Charadriiformes in our analyses, we consistently support that this order is not basal within Neoaves (*24*) and thus refute the hypothesis that transitional shorebirds gave rise to all modern birds (*7*). Our phylogeny revealed a highly supported water bird clade (blue, node H, Fig. 2) (*3*, *14*), including members of the Pelecaniformes (totipalmate birds), Ciconiiformes (storks and allies), Procellariiformes (tube-nosed birds), Sphenisciformes (penguins), and Gaviiformes (loons). Basal to the water birds were two clades of terrestrial and arboreal taxa

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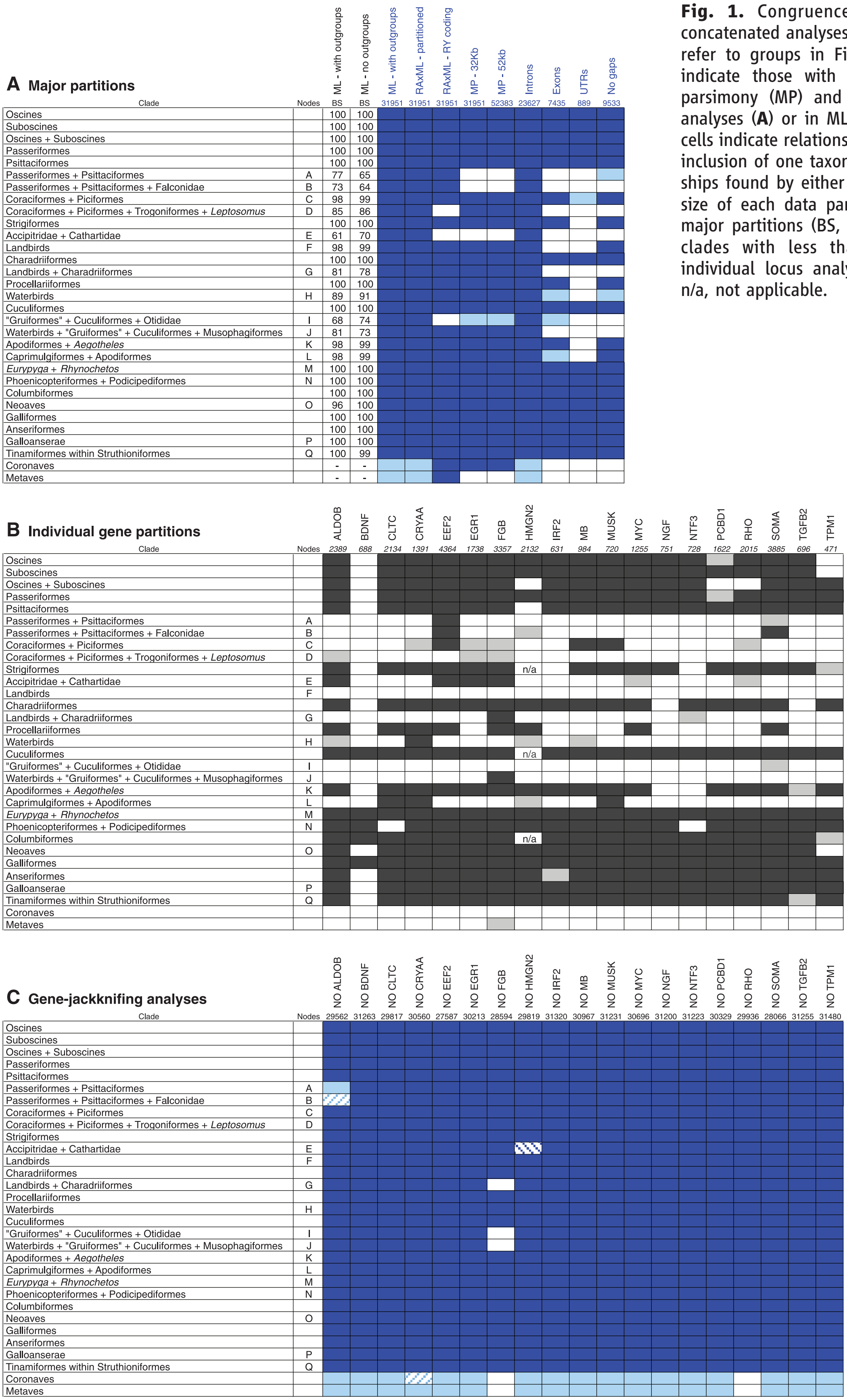

Fig. 1. Congruence of clades as determined from concatenated analyses and multiple data partitions. Nodes refer to groups in Fig. 2. Dark blue or dark gray cells indicate those with relationships present in maximum parsimony (MP) and ML [GARLI (*31*) and RAxML (*32*)] analyses (**A**) or in ML (**B** and **C**); light blue or light gray cells indicate relationships present with the exception of or inclusion of one taxon; and striped cells indicate relationships found by either GARLI or RAxML, but not both. The size of each data partition is listed below its name. (A) major partitions (BS, bootstrap support; dashes represent clades with less than 50% bootstrap support); (B) individual locus analyses; (C) gene-jackknifing analyses. n/a, not applicable.

(node J, Fig. 2): Musophagiformes (turacos) and a clade (gray, node I, Fig. 2) including core Gruiformes (rails, cranes, and allies), Cuculiformes (cuckoos), and Otididae (bustards, which are typically considered as belonging to Gruiformes). These latter relationships were also largely dependent on the presence of *FGB* (Fig. 1) and require further study to determine their validity.

One of our most important findings was that several well-accepted orders were not monophyletic. Our analyses provided strong support that (i) Tinamiformes (tinamous) are found

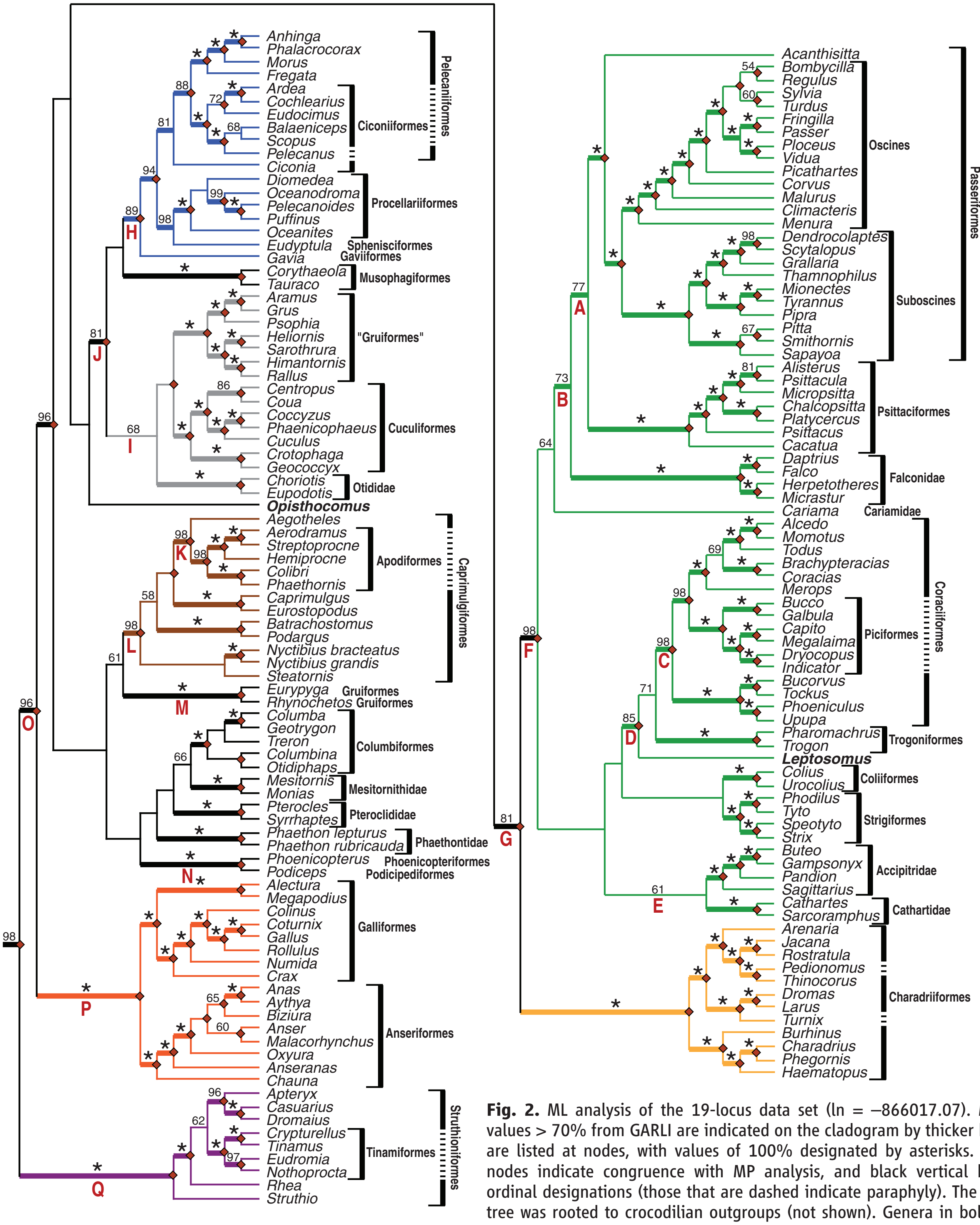

Fig. 2. ML analysis of the 19-locus data set (ln = –866017.07). ML bootstrap values > 70% from GARLI are indicated on the cladogram by thicker branches and are listed at nodes, with values of 100% designated by asterisks. Diamonds at nodes indicate congruence with MP analysis, and black vertical bars refer to ordinal designations (those that are dashed indicate paraphyly). The phylogenetic tree was rooted to crocodilian outgroups (not shown). Genera in bold are icertae sedis. Branch colors represent major clades supported in this study: land birds (green), charadriiforms (yellow), water birds (blue), core gruiforms and cuckoos (gray), apodiforms and caprimulgiforms (brown), galloanserae (orange), and paleognaths (purple). Large capital letters indicate groups discussed in the text and Fig. 1.

within Struthioniformes (ostriches and allies; purple, node Q, Fig. 2), (ii) Apodiformes (hummingbirds and swifts) are found within Caprimulgiformes (nightjars and their allies; brown, node L, Fig. 2), and (iii) Piciformes are found within Coraciiformes (node C, Fig. 2). Typical Pelecaniformes and Ciconiiformes [sensu (*13*, *25*)] were intermixed in a clade (Fig. 2) that excludes one traditional pelecaniform family: the Phaethontidae (tropicbirds). The Gruiformes represented at least four distinct clades in our tree (Fig. 4), depending on the circumscriptions of this order [reviewed in (*6*)]. Finally, Falconidae and Accipitridae (hawks and osprey) formed distinct clades in all analyses, rather than a monophyletic Falconiformes (Fig. 2) (*18*).

Several disparate taxa were robustly placed in our analyses. Cariamidae (seriemas) has traditionally been classified as a gruiform, although convergence with Falconiformes was noted (*6*). We found strong support for placing Cariamidae within land birds near other raptorial groups. *Leptosomus* (cuckoo roller) is generally placed within Coraciiformes, though a relationship with Falconiformes has also been suggested (*6*). Our data set placed *Leptosomus* sister to a clade including Piciformes, Coraciiformes, and Trogoniformes (node D, Fig. 2).

Our results suggest resolution of some controversial groupings. For example, Cathartidae (New World vultures)—traditionally placed within Falconiformes—were previously allied with Ciconiidae (storks) (*6*). However, our phylogeny demonstrated no affinity with storks [see also (*3*, *18*, *26*)] and instead strongly supported placement of Cathartidae within the land birds (usually with Accipitridae). We support that *Turnix* (buttonquail) belongs within the Charadriiformes (*3*, *4*, *27*) and that Podicipediformes (grebes) and Phoenicopteriformes (flamingos; node N, Fig. 2) (*14*) are sister taxa. Finally, we recovered a sister relationship between *Rhynochetos* (kagu) and *Eurypyga* (sunbittern) (node M, Fig. 2) (*28*): two monospecific and geographically disparate families that grouped outside of the core Gruiformes.

The previously proposed division of Neoaves into Coronaves and Metaves is driven by two loci (*4*) in our analyses (Fig. 1) and may not represent the species tree. Many taxa assigned to Metaves are composed of small numbers of closely related extant species, including Mesitornithidae (mesites), Phaethontidae, Pteroclididae (sandgrouse), and Columbiformes (pigeons and doves). The difficulty in placing them may be driven by long, unbreakable branches leading to the tips (Fig. 3). The enigmatic *Opisthocomus* (hoatzin) still cannot be confidently placed, but some putative sister relationships can be rejected (*29*).

Modern birds occupy a wide diversity of niches and exhibit a variety of behaviors. The broad structure of our phylogeny suggested diversification along general ecological divisions, such as water birds, shorebirds, and land birds. However, adaptations to these environments clearly arose multiple times (*4*), because many aquatic birds were not part of the water bird clade (e.g., tropicbirds, flamingos, and grebes) and terrestrial birds were found outside of the land bird clade (e.g., turacos, doves, sandgrouse, and cuckoos). Our phylogeny also indicated several distinctive niches, such as nocturnal (owls, nightjars, and allies), raptorial (falcons, hawks, eagles, New World vultures, seriema, and owls), or pelagic (tubenosed birds, frigatebirds, and tropicbirds) lifestyles, have evolved multiple times. Furthermore, our results reinterpret the evolution of various adaptations (e.g., the diurnal Apodiformes evolved from nocturnal/crepuscular Caprimulgiformes, and flighted Tinamiformes arose within the flightless Struthioniformes) and biogeographic patterns (e.g., the New Caledonian kagu and Neotropical sunbittern are sister taxa).

Given the number of nonmonophyletic groups in our study, we compared our results with major classifications [supporting online material (SOM) text]. Unexpectedly, roughly the same percentage (35%) of orders defined by different classifications (*13*, *25*, *30*) was not monophyletic relative to the results of our study (Fig. 4). Some orders, such as Gruiformes and the broadly encompassing Ciconiiformes [sensu (*30*)], were particularly problematic. Other traditional orders were not monophyletic because of the exclusion or inclusion of one or a few taxa (e.g., placing *Turnix* within Charadriiformes contradicts all three classifications). Only six orders were defined consistently across taxonomies and monophyletic in our study (Fig. 4). Given our results, conclusions from comparative studies that depended upon these classifications may need to be re-evaluated in light of this understanding of avian evolution.

Deciphering the roots of the avian tree of life has been a lingering problem in evolutionary biology. The inclusion of multiple loci with diverse rates of evolution, particularly the large proportion of rapidly evolving introns, yielded a well-supported phylogenetic tree at multiple taxonomic depths. Although some higher-level avian relationships remain unresolved, simulations suggest that additional sequence data from rapidly evolving loci may resolve these remaining questions (*1*). It is also evident that future classifications will

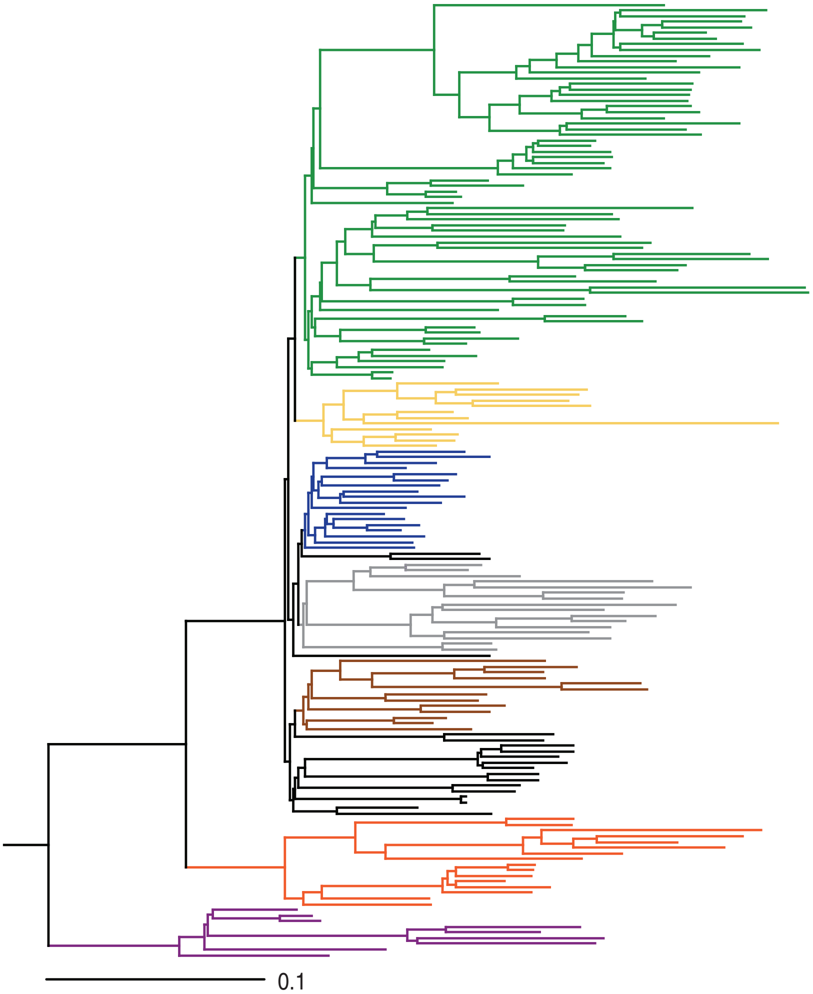

Fig. 3. ML phylogram demonstrating the short internodes at the base of Neoaves and highlighting certain extreme examples of rate variation across avian lineages. Colors are as in Fig. 2. Scale bar indicates substitutions per site. Figure S1 shows the phylogram with taxon names.

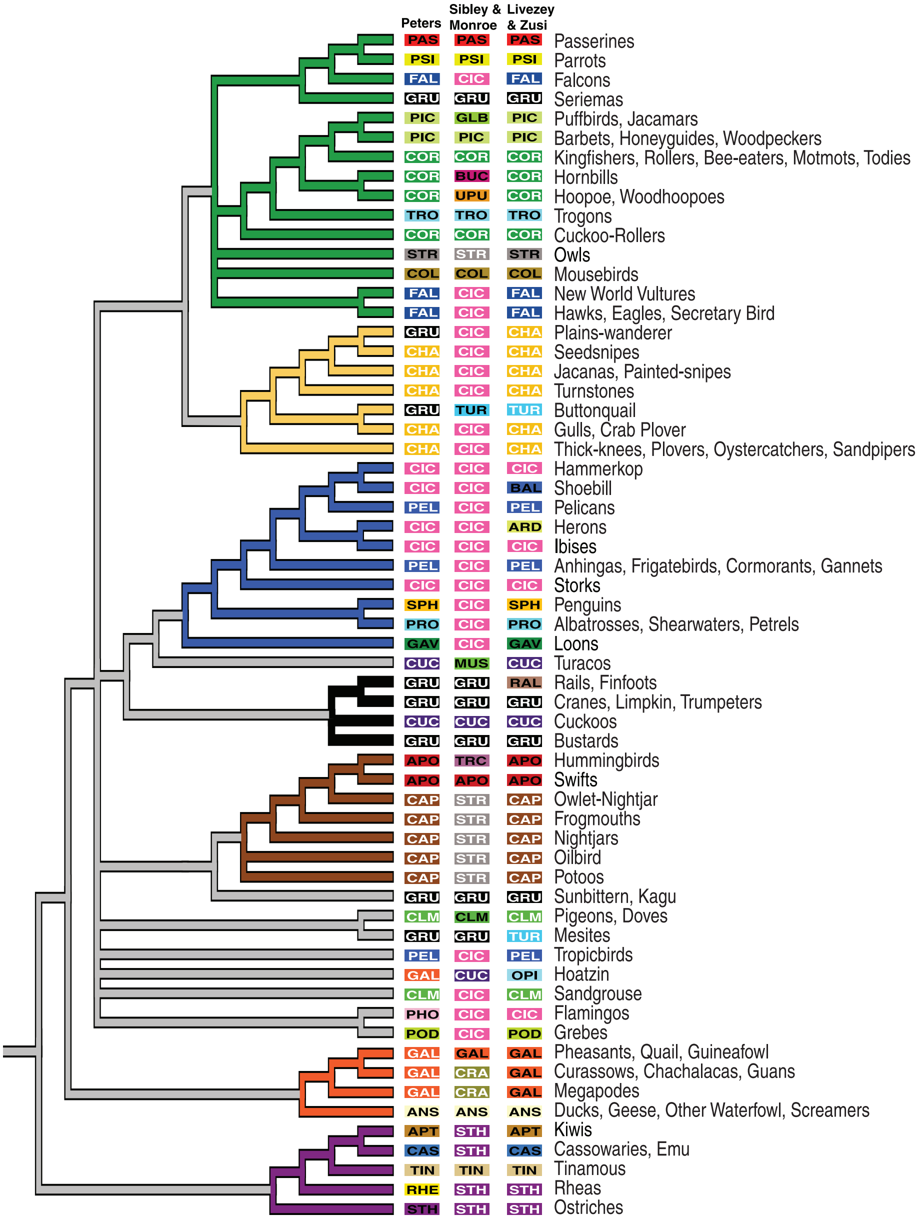

Fig. 4. Our phylogeny differs from and agrees with previous classifications. We merged well-supported (>70% bootstrap values) monophyletic clades at the tips with the same ordinal designation across all three classifications (e.g., 24 species called Passerines). Only higher relationships supported by bootstrap values >50% are shown. Colors are as in Fig. 2. Color bars to the right of the tree show membership in three different classifications: Peters' (*25*) (left), Sibley and Monroe's (*30*) (middle), and Livezey and Zusi's (*13*) (right). Black text within the bars indicates monophyletic orders in our phylogeny, whereas white text within the bars indicates nonmonophyletic orders. Ordinal name codes: ANS (Anseriformes), APO (Apodiformes), APT (Apterygiformes), ARD (Ardeiformes), BAL (Balaenicipitiformes), BUC (Bucerotiformes), CAP (Caprimulgiformes), CAS (Casuariiformes), CHA (Charadriiformes), CIC (Ciconiiformes), CLM (Columbiformes), COL (Coliiformes), COR (Coraciiformes), CRA (Craciformes), CUC (Cuculiformes), FAL (Falconiformes), GAL (Galliformes), GAV (Gaviiformes), GLB (Galbuliformes), GRU (Gruiformes), MUS (Musophagiformes), OPI (Opisthocomiformes), PAS (Passeriformes), PEL (Pelecaniformes), PIC (Piciformes), POD (Podicipediformes), PRO (Procellariiformes), PSI (Psittaciformes), RAL (Ralliformes), RHE (Rheiformes), SPH (Sphenisciformes), STH (Struthioniformes), STR (Strigiformes), TIN (Tinamiformes), TRC (Trochiliformes), TRO (Trogoniformes), TUR (Turniciformes), and UPU (Upupiformes).

change dramatically, based on our phylogenetic study, and that our results will stimulate comparative studies to address the growing number of questions regarding the evolution of birds.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/320/5884/1763/DC1
Materials and Methods
SOM Text
Figs. S1 to S3
Tables S1 to S3
References

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A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century

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Spatial fingerprints of climate change on biotic communities are usually associated with changes in the distribution of species at their latitudinal or altitudinal extremes. By comparing the altitudinal distribution of 171 forest plant species between 1905 and 1985 and 1986 and 2005 along the entire elevation range (0 to 2600 meters above sea level) in west Europe, we show that climate warming has resulted in a significant upward shift in species optimum elevation averaging 29 meters per decade. The shift is larger for species restricted to mountain habitats and for grassy species, which are characterized by faster population turnover. Our study shows that climate change affects the spatial core of the distributional range of plant species, in addition to their distributional margins, as previously reported.

Recent warming has induced biological and ecological responses from animals and plants throughout the world (*1*–*3*). Consistent responses to global warming or "fingerprints" are apparent in the phenology and distribution of species (*1*–*5*). For plants, invertebrates, and vertebrates, climate change has strongly influenced distribution and abundance at range margins both in latitude (polar margins) (*5*–*8*) and in elevation (upper margins) (*5*, *9*–*11*), and even in depth for marine fishes (*8*). Shifts at the upper edge of altitudinal range agree with the hypothesis of an upward trend to escape rising temperatures (*12*–*14*). Changes in range limits, however, are just one, albeit important, expression of the likely consequences of climate change. More subtle changes within the ranges of species are also likely and, although poorly explored as yet, might have important ecological and evolutionary consequences. Assuming niche conservatism over evolutionary time (*15*), we tested for large-scale (across temperate and Mediterranean mountain forests in west Europe), long-term (over the 20th century), and multispecies (through an assemblage of 171 species) climate-related responses in forest plant altitudinal distributions. We analyzed species responses by measuring shifts in the altitudinal position of species' maximum probability of presence within their distribution, instead of focusing on distributional extremes. Additionally, we tested for the effect of ecological and life history traits on the magnitude of the response to climate warming (*16*). In particular, we tested whether species restricted to mountain areas (*10*–*12*, *17*, *18*) and/or fast generation times (*19*) are particularly sensitive to temperature changes.

We studied species in forest communities found between lowland to the upper subalpine vegetation belt (0 to 2600 m above sea level) over six mountain ranges in west Europe (the Western Alps, the Northern Pyrenees, the Massif Central, the Western Jura, the Vosges, and the Corsican range). Climatic change in France has been characterized by increases in average temperature of far greater magnitude than increases in the world mean annual temperature, of about 0.6°C over the 20th century (*20*), reaching up to 0.9°C (*21*) and even close to 1°C in the alpine region since the early 1980s (*22*). From two large-scale floristic inventories (about 28,000 surveys) (*23*), we extracted two well-balanced subsamples, including 3991 surveys each, carried out across the studied mountain ranges (see fig. S1 for surveys location). The first subsample included surveys carried out before the mid-1980s (1905–1985), and the other one, after 1985 (1986–2005) (see fig. S2 for altitudinal distribution of surveys). We chose this temporal threshold because the analysis of yearly mean surface temperature anomalies between 1965 and 2005 shows that in 1986 the studied mountain ranges experienced a temperature regime shift (Fig. 1A), staying above the average baseline conditions. In contrast, analysis of annual precipitation anomalies between 1965

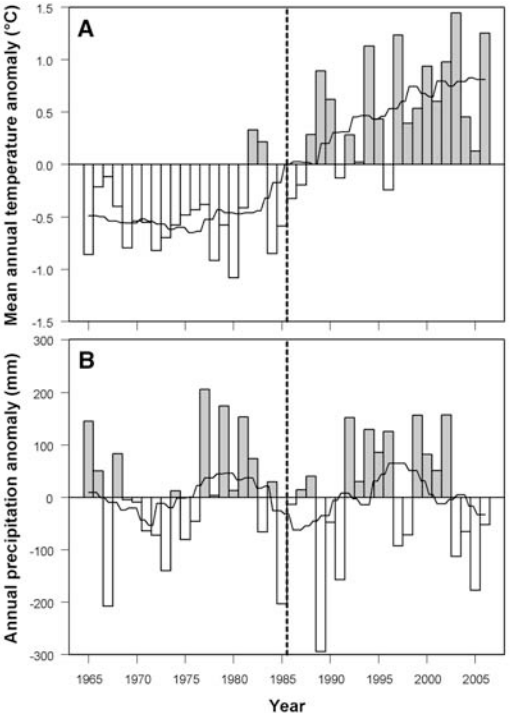

Fig. 1. Climatic trends from 1965 to 2006. (**A**) Yearly mean surface temperature anomalies (using overall mean temperature as baseline) and (**B**) annual precipitation anomalies (using overall mean annual precipitation as baseline) averaged for 73 elevation sites in the French mountains ranging in altitude from 10 to 2010 m above sea level. Solid gray bars refer to positive anomalies, whereas open bars refer to negative ones. The solid curve is the smoothed average with use of a 10-year filter. The vertical dotted lines mark the split between the two studied periods. Data have been gathered from the French National Climatic Network (Météo-France).

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