Phylogeny and Evolution of the Passerine Birds

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The passerines (Order Passeriformes) comprise one of the most diverse groups of birds alive today. Highly varied in structure, behavior, and ecology and beautiful in song and plumage, passerines have historically generated considerable interest among scientists and the public alike. Consisting of roughly 5700 species, or nearly 60% of extant birds (Sibley and Monroe 1990), the passerines are disproportionately represented among birds, as are, for example, beetles among insects and rodents among mammals. Hence, like these groups, passerines have been the subject of intense study by evolutionary biologists. In the last two decades, research on the evolution of the passerines has yielded insight into a variety of issues, including their monophyly, phylogeny, and adaptive radiation, as well as the factors that may be responsible for their great diversity. These efforts have led to a revolution in ideas about passerine history and its ecological and evolutionary implications.

Passerines occur worldwide in every terrestrial habitat except permanent ice and snow, and they occupy a remarkably diverse set of ecological niches. So numerous are passerines that ornithologists commonly divide birds into passerines and nonpasserines, the first a formal taxonomic group and the second but an informal term of exclusion. The passerines in turn are divided into two subgroups. The oscines (songbirds) are characterized by a distinctive syrinx, or vocal organ (Figure 1d), and by associated complex vocalizations, which are often learned through imitation. The second group, the suboscines, have less complex vocal organs (Figures 1a and 1b) and their songs do not appear to be learned by imitation. We point out the oscine–suboscine division for two reasons. First, it is a phylogenetically important distinction that we will refer to often. Second, and more fundamental, the anatomical distinctions upon which the oscine–suboscine division is based illustrate the central approach used in evolutionary studies by biologists interested in the origin and nature of organismal diversity—the comparative approach.

Systematics and the comparative approach

Modern studies in systematics involve between-species comparisons of anatomical, molecular, and behavioral characters, the patterns of which are used to establish evolutionary relationships among lineages. At the most basic level, comparative systematic inquiry can be considered a two-step process, regardless of types of characters or methods of analysis. The first step entails an estimation of a group's phylogeny, or the pattern of branching of lineages through time, by analysis of character variation among the group's members. Estimates of phylogeny are typically represented as branching or tree diagrams, with each branching event corresponding to the splitting (speciation) of an ancestral species into descendent, or daughter, species. The second step involves the use of estimates of phylogeny to gain insight into fundamental evolutionary processes, such as modes of speciation, the roles of natural selection and genetic drift in evolutionary change, and the ecological mechanisms that influence levels of biological diversity at global, continental, landscape, and community scales. Both steps require extensive comparison among lineages,

> INDEPENDENT METHODS OF PHYLOGENETIC ANALYSIS HAVE PRODUCED A WELL-SUPPORTED HYPOTHESIS OF PASSERINE PHYLOGENY, ONE THAT HAS PROVED PARTICULARLY USEFUL IN ECOLOGICAL AND EVOLUTIONARY STUDIES

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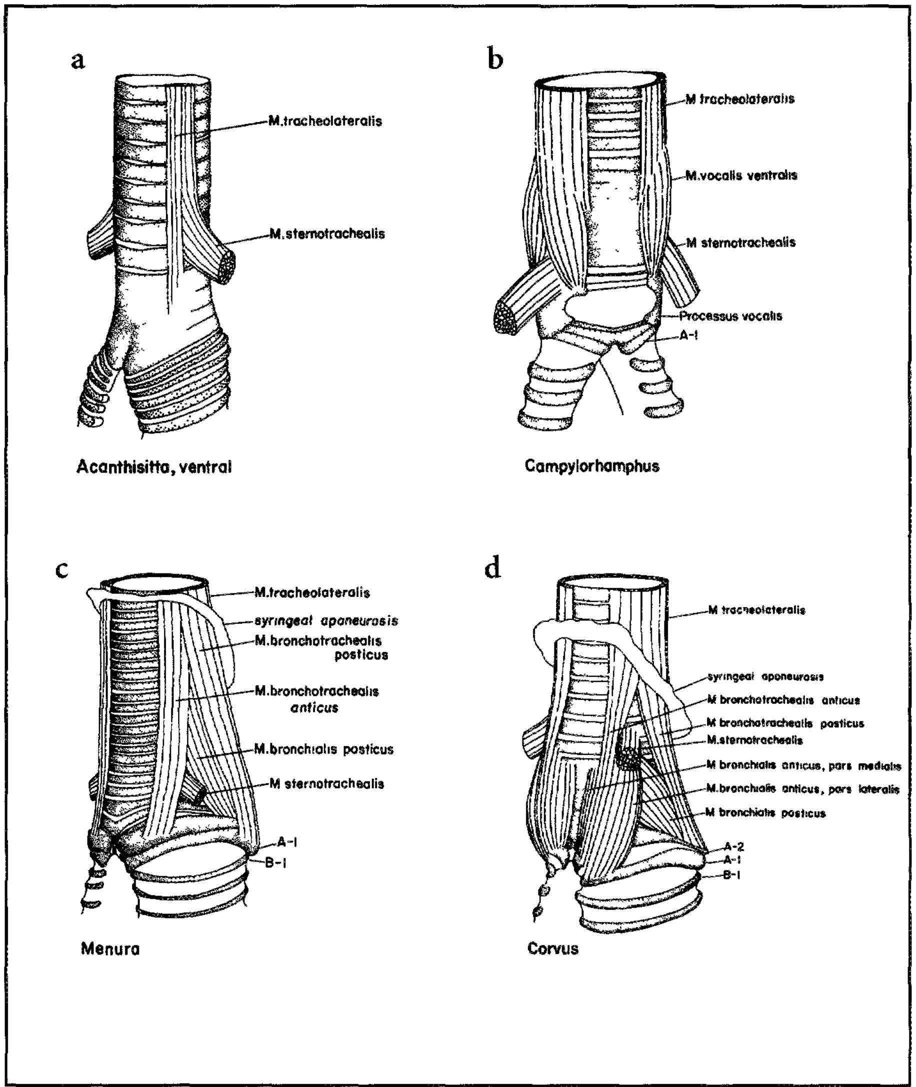

Figure 1. Vocal organs of passerine birds. Syringes (vocal organs) of representative passerines are located at the juncture of the trachea and bronchi. (a) Acanthisitta *(New Zealand wren) showing a relatively simple syrinx lacking complex musculature; (b)* Campylorhamphus *(woodcreeper) illustrating a tracheophone syrinx; (c)* Menura *(lyrebird) showing an atypical oscine syrinx; (d)* Corvus *(crow) showing a typical oscine syrinx. Reprinted from* The Morphology of the Syrinx in Passerine Birds, *by Peter L. Ames (1971), courtesy of Peabody Museum of Natural History, Yale University (a–c), and Academic Press (d).*

using a variety of explicit analytical techniques.

One method for inferring phylogeny involves the analysis of discretely defined characters, most frequently by cladistic methods in which modifications of the ancestral state of a character provide evidence of phylogenetic history. The ancestral state may be retained by some members of a group, whereas other members may possess a modified, or derived, state of the ancestral condition. Because the derived state evolved later in evolutionary history than the ancestral state, those species that possess the derived state should be more closely related to each other than to any other members of the group. Underlying this argument is the idea that heritable modifications (derived states) evolved in an ancestral species will be passed on to all descendants of that species through speciation. Such derived states shared among species are used to delimit monophyletic subgroups (clades) consisting of an ancestral species, all of its descendants, and only those descendants. The concept of monophyly is a central, precise formulation of the traditional biological notion of a "natural" group.

Another way to estimate phylogeny relies on the analysis of genetic distances between species, without direct reference to ancestral or derived states. For birds, the most commonly used genetic distances are based on molecular comparisons of allozymes (allelic isozymes), using gel electrophoresis, or single-copy nuclear DNA sequences, using solution DNA–DNA hybridization. The latter technique has been particularly important in avian systematics by virtue of its extensive application by Charles G. Sibley and his students. DNA hybridization techniques compare a large number of DNA sequences to generate a matrix of species-by-species distances, the pattern of which provides evidence of phylogeny. Although DNA hybridization phylogenies are not based on direct knowledge of the actual sequence of nucleotides, the pattern of between-species distances in expectation corresponds to the underlying pattern of shared derived nucleotide substitutions (Bledsoe and Sheldon 1990). This correspondence forms the basis for estimating phylogenies from genetic distance matrices generated from DNA hybridization data.

Passerine monophyly

The passerines, like many traditionally recognized groups of species, were established without explicit use of the concept of monophyly as defined above. Some traditional taxa are monophyletic and some are not. Do the passerines form a monophyletic group? Stated another way, are any of the features that were used to define the group in reality derived states shared among passerines and only passerines (Raikow 1982)? Analysis indicates that of 18 characters that previous workers used in diagnosing the group, 13 either describe passerine anatomy inaccurately or are of more general (ancestral) occurrence within birds, whereas 5 describe anatomy accurately and are derived (novel) within birds as a whole. The latter characters support the hypothesis of passerine monophyly (Table 1); the others are uninformative or misleading (Raikow 1982).

Table 1. Characters that have been proposed to support passerine monophyly.

Character	Explanation
Supportive traditional characters	
Palate aegithognathous	Arrangement of bones
Tensor propatagialis brevis tendon "passerine"	Wing muscle
Spermatozoa bundled, with coiled head, large acrosome	Cell structure
Hallux and its claw large	Hind toe
Type VII deep plantar tendons	Leg muscles
Supportive recent characters	
M. pubo-ischio-femoralis with cranial/caudal bellies	Leg muscle
Intrinsic muscles of forward toes lost	Foot muscles
DNA hybridization	Genetic distance
Nonsupportive traditional characters	
Atlas perforated	Vertebral structure
Only left carotid artery present	Vascular structure
Oil gland nude	Feather tuft lacking
Wing eutaxic	Feather arrangement
Intestinal ceca small	Outpocketing of gut
Expansor secundariorum	Wing muscle
Biceps slip lacking	Wing muscle
Iliofemoralis externus lacking	Leg muscle
Ambiens lacking	Leg muscle
Iliofemoralis lacking	Leg muscle
Foot anisodactyl	Three toes forward, one back
Phalangeal formula 2-3-4-5	Toe bones
Hallux incumbent	Hind toe not elevated

The statement that the passerines are monophyletic is a hypothesis, like all phylogenetic proposals. A key component of the advancements in systematics over the last two decades has been the recognition of the importance of testing hypotheses of monophyly and the development of various approaches for doing so. One approach involves the use of additional characters to test the robustness of a hypothesized phylogeny (see Kluge 1997). In the case of the passerines, new data from the hindlimb musculature have identified additional derived characters (Raikow 1982), which have subsequently been discovered in both the oscine and suboscine passerines (Raikow 1987, 1993). Another test seeks congruence between the results of independent studies (see Bledsoe and Raikow 1990), especially when these results involve different kinds of evidence. In addition to the morphological data that support the hypothesis of passerine monophyly, support is also provided by extensive DNA hybridization data (Sibley and Ahlquist 1990) and a smaller mitochondrial DNA data set (Mindell et al. 1997). Because the enlarged anatomical data set and the new DNA studies strengthen the contention that the passerines are monophyletic, scientists are now in a position to consider what form their history may have taken and what that history means for the analysis of ecological and geographic patterns among the passerines.

Passerine phylogeny

Results from studies undertaken in the past dozen years have greatly improved scientists' understanding of passerine phylogeny. Morphological cladistic analyses and DNA hybridization studies have independently generated highly similar branching patterns for the basal divisions of the passerine tree (Figure 2a; Sibley and Ahlquist 1985, 1990, Raikow 1987, Prum 1993). The branching patterns differ markedly from those implied by classifications in use merely a few decades ago (Figure 2b). Gone is the once-popular notion of the "primitiveness" of the broadbills

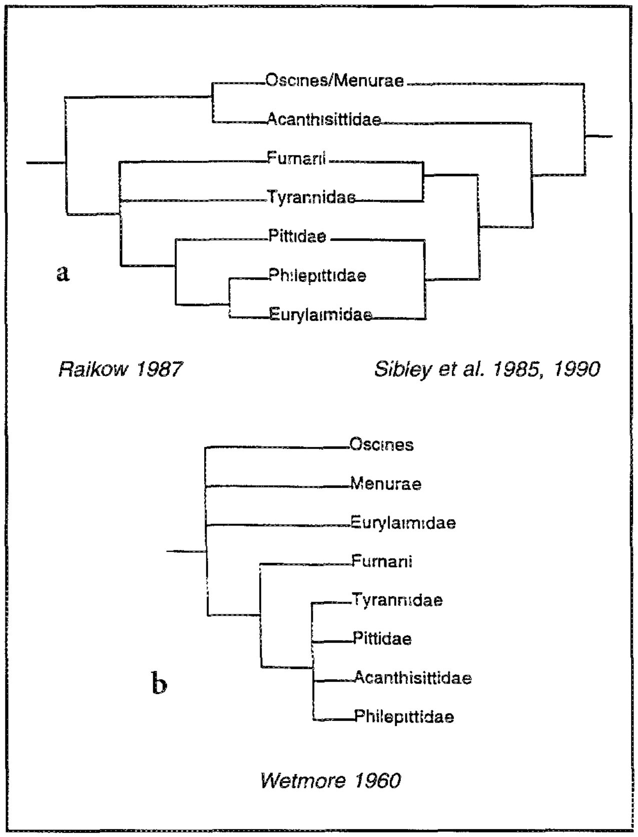

Figure 2. Passerine phylogeny. (a) Hypotheses of the phylogenetic relationships of major passerine groups proposed on the basis of a morphological cladistic analysis, using maximum parsimony and discrete characters (left, Raikow 1987), and DNA hybridization (right, Sibley and Ahlquist 1985, 1990). The trees differ only in resolution (regions where the data could not fully resolve the branching pattern) and the position of the New Zealand wrens (Acanthisittidae). (b) Indented structure of the passerine classification of Wetmore (1960). See Table 2 for common names of the groups. The Menurae consists of the lyrebirds and scrub-birds. Figure redrafted from Raikow (1987).

Table 2. Major groups of passerine birds.

Group	Genera	Species	Distribution
Suboscines			
Eurylaimidae (Broadbills)	8	14	Southeast Asia, Africa (2 spp.)
Pittidae (Pittas)	1	31	Southeast Asia, Africa (1 sp.), and Australia and New Guinea (2 spp.)
Philepittidae (Asities)	2	4	Madagascar
Tyrannidae (New World flycatchers)	146	537	New World, primarily South America
Furnarii (Tracheophone Passerines)	131	560	New World, primarily South America
Acanthisittidae (New Zealand wrens)	2	4	New Zealand
Oscines (only two radiations listed)			
Corvida	229	1101	Primarily Australia and New Guinea
New World nine-primaried songbirds	240	993	Primarily New World, many South American

(Eurylaimidae) and the lyrebirds and scrub-birds (Menuridae; sensu Sibley and Monroe 1990). The suboscines consist of two monophyletic groups, the New World suboscines and the Old World suboscines, which, as their names imply, divide along geographic lines. In addition, the hierarchical positions of several groups are now specified. As a result, the linear classifications of previous eras, which held no clear phylogenetic meaning, have been replaced with hierarchical classifications (Raikow 1987, Sibley and Monroe 1990) based on phylogenetic understanding. Furthermore, the estimates of phylogeny in Figure 2 provide the basis for the analysis of passerine geography, diversity, and adaptive radiation.

These hypotheses of passerine phylogeny permit a general analysis of the geographic distributions of the major groups, their relative numbers of species, and their degrees of anatomical variety (Table 2). Although the picture is complex, several patterns emerge. The Old World suboscines (sensu Raikow 1987) subsume 49 species of substantial anatomical variety, as measured either indirectly by the number of genera or directly by the extent of muscular variation (Raikow 1987). The Old World suboscines are concentrated in southeastern Asia and are species-poor, despite their high degree of morphological distinctiveness. In contrast, the New World suboscine radiation is vast, subsuming 1098 species (roughly 22 times the diversity of Old World suboscines), all endemic to the New World (primarily to South America) and exhibiting great variety in bill form, myology, plumage, and behavior. In addition, the New World and Australia each have a large oscine radiation of substantial anatomical variety—the New World nine-primaried oscines and the Australo-Papuan Corvida (sensu Sibley and Ahlquist 1990).

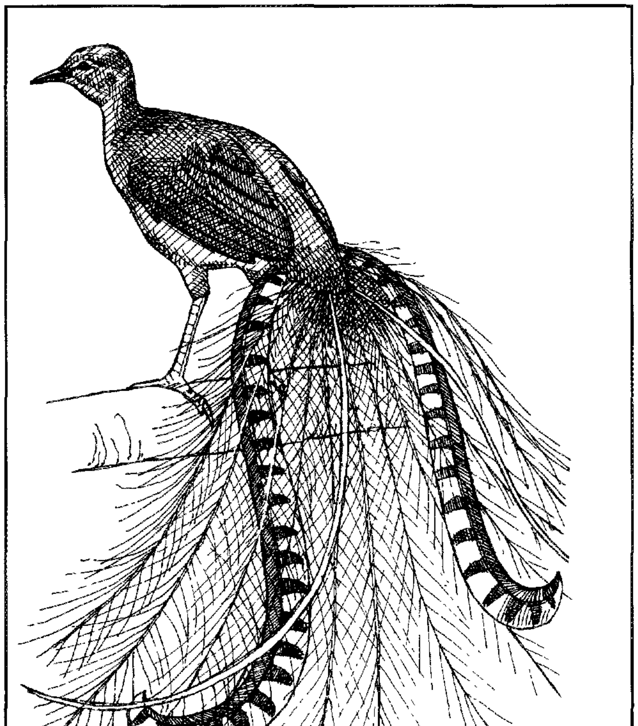

Figure 3. Superb lyrebird (*Menura novaehollandiae*). A member of the Menuridae. Reprinted from* A Dictionary of Birds, *by Bruce Campbell and Elizabeth Lack (1985). Courtesy of the British Ornithologists' Union.

The wide distribution and extensive anatomical variety of the Old World suboscine clade suggest that they represent remnants of a previously more speciose radiation, with relict groups on Madagascar, in tropical Africa, and in southeastern Asia. In contrast, the New World suboscines and nine-primaried oscines have radiated extensively, presumably while South America was geographically isolated during much of the Cenozoic. Likewise, the Corvida radiation probably occurred during Australia's long period of isolation. Notably, with the exception of the presumably recent entries of pittas (Pittidae) and the possible exception of the New Zealand wrens (Acanthisittidae), the Australo-Papuan region lacks suboscines.

The above propositions must be regarded as tentative, in part because no clear and simple geographic picture of passerine evolution emerges, and in part because debate surrounds the positions of two important Australo-Papuan groups: the lyrebirds (Figure 3) and scrub-birds (Figure 4) of Australia and the New Zealand wrens (Figure 5). The lyrebirds and scrub-birds were considered by Feduccia and Olson (1982) to represent remnants of a sub-

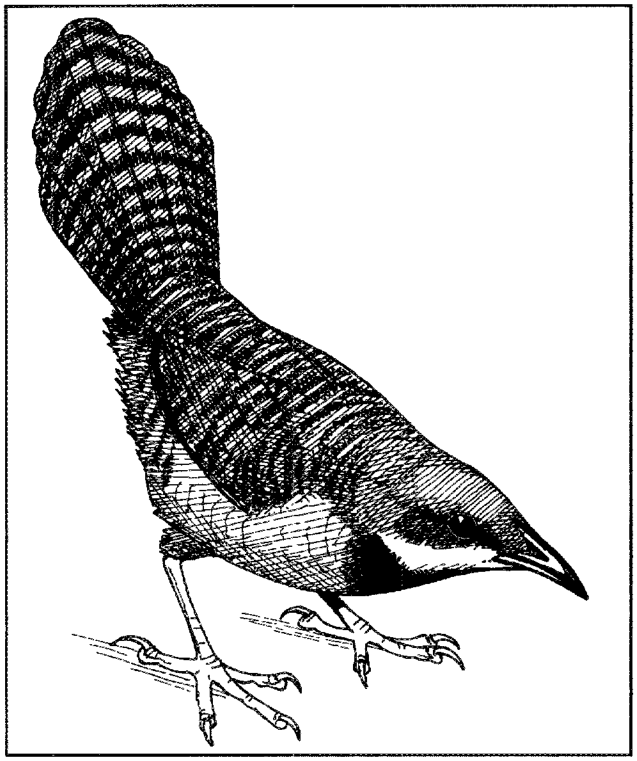

*Figure 4. Noisy scrub-bird (*Atrichornis clamosus*). A member of the Menuridae. Reprinted from* A Dictionary of Birds, *by Bruce Campbell and Elizabeth Lack (1985). Courtesy of the British Ornithologists' Union.*

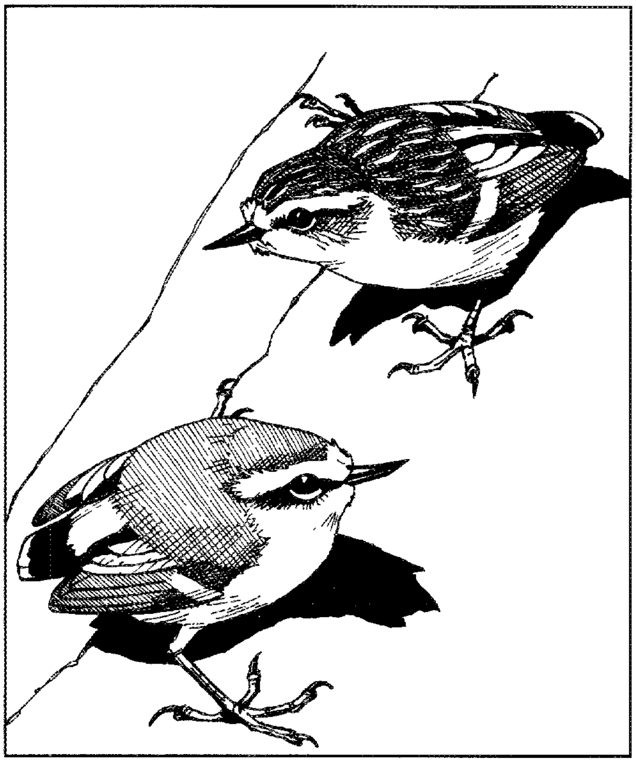

*Figure 5. Rifleman (*Acanthisitta chloris*). A member of the New Zealand wrens (Acanthisittidae). Reprinted from* A Dictionary of Birds, *by Bruce Campbell and Elizabeth Lack (1985). Courtesy of the British Ornithologists' Union.*

oscine radiation. However, their inclusion in the oscine clade is supported by a substantial amount of anatomical and molecular data (syrinx, Ames 1971; musculature, Raikow 1985; DNA hybridization, Sibley and Ahlquist 1990; protein data, Christidis and Schodde 1991). More controversial are the New Zealand wrens. They lack the distinctive syrinx that delimits the oscines, and their stapes (a bone of the middle ear) does not have the bulbous, derived shape that delimits the suboscines (Feduccia 1975). The New Zealand wrens thus disrupt the otherwise neat division of the passerines into oscines and suboscines. Sibley and Ahlquist (1990) placed the New Zealand wrens with the rest of the suboscines, but in doing so they assumed a molecular clock, and they did not test that assumption. Analysis without the restrictive clock assumption (Sibley and Ahlquist 1990) did not resolve the relationships of the New Zealand wrens.

Anatomical evidence supports a different position for the New Zealand wrens. Raikow (1987) placed them as the sister group of the oscines, based on the absence of the distal belly of a leg muscle, M. flexor perforatus digiti IV. The condition is almost certainly derived, as cladistic analysis suggests, because the belly reappears in oscines as an atavistic anomaly (Raikow 1987). Such anomalies are best interpreted as the result of abnormal activation of a conserved genetic mechanism (Raikow 1975). The most parsimonious interpretation is that the condition evolved only once. Hence, the condition provides support for sister-group status of the oscines and New Zealand wrens (Raikow 1987).

These patterns of phylogeny, geography, and diversity hint at a Southern Hemisphere origin of the passerines, as suggested by Feduccia and Olson (1982) on primarily geographic grounds, with subsequent extinction of basal lineages in the Australo-Papuan region and extensive radiation of isolated South American and Australian groups. A Gondwanaland origin of passerines would be consistent with a recent combined analysis of paleontological and molecular evidence (Cooper and Penny 1997) suggesting a Cretaceous origin of many modern avian lineages, including the passerines. Although the new work will require critical inspection, an independent molecular analysis by Mindell et al. (1997) also points to an early origin of the passerines. Both Mindell et al. (1997) and Cooper and Penny (1997) noted potential problems with their analyses, but the main point stands: The appreciable advancement in our understanding of passerine phylogeny now permits the formation and assessment of hypotheses that could not have been proposed just two decades ago.

Passerine adaptive radiation

Avian biology provides two textbook examples of adaptive radiation: Darwin's finches and the Hawaiian honeycreepers. The small numbers of species in these insular groups

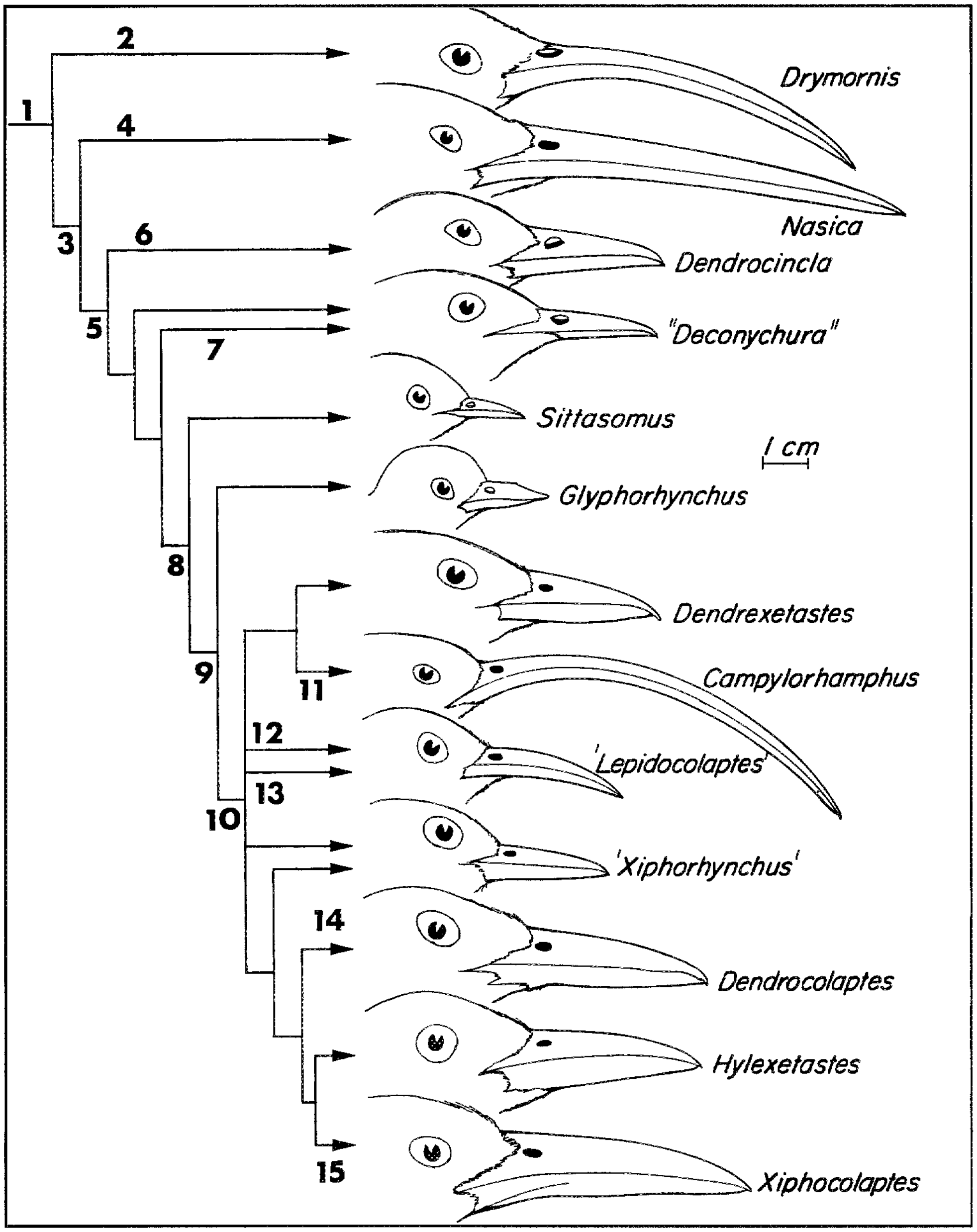

Figure 6. Evolution of woodcreeper bills. One species is illustrated from each genus, with the phylogenetic branching pattern (Raikow 1994a) resolved to the level of genus. Illustrations are to scale. 1, bill long, gonys (ventral midline of lower mandible) ridged; 2, bill strongly decurved full length; 3, bill depressed; 4, nasal operculum absent, bill slightly decurved full length; 5, bill length intermediate, culmen (dorsal midline of upper mandible) ridged; 6, bill straight, tip of maxilla (upper mandible) decurved; 7, bill straight, tip of maxilla (upper mandible) decurved; 8, bill short; 9, culmen rounded, gonys rounded; 10, nostril roundish, nasal operculum absent, bill compressed, bill length intermediate; 11, bill strongly decurved full length, bill length long, width of bill uniform, not tapered; 12, bill slightly decurved full length; 13, bill slightly decurved full length; 14, maxillary tomium notched, bill depressed, culmen ridged, gonys ridged; 15, bill slightly decurved full length, bill long.

facilitated the analysis of their adaptive radiation when methods of hypothesizing phylogeny were still inexact. By "adaptive radiation" we mean "evolutionary divergence of members of a single phylogenetic line into a variety of different adaptive forms; usually with reference to divergence in the use of resources or habitats" (Futuyma 1986, p. 550). The recent development of cladistic analysis and various molecular methods of phylogeny reconstruction now per sage that follows, we discuss the general implications of recent phylogenetic studies of three such continental radiations: the Neotropical woodcreepers, the New World nine-primaried songbirds, and the Australo-Papuan oscines.

The woodcreepers. Research in our laboratory over the past decade has concentrated on the Furnarii, a Neotropical suboscine assemblage of some 560 species. This group is monophyletic, based on the possession of a unique, derived syrinx (Figure 1b). The Furnarii provide an example of a large-scale continental adaptive radiation. Our most intense investigations of the Furnarii have focused on the woodcreeper subgroup (Dendrocolaptinae), which consists of 13 genera and 50 species. The hypothesis that the woodcreepers form a monophyletic group is supported by both morphological (Raikow 1994a) and molecular (Sibley and Ahlquist 1990) evidence.

All woodcreepers can climb and forage on vertical surfaces. During climbing, they are supported by the sharply curved claws of their forward toes and by their stiffened tails. Anatomical analysis (Raikow 1994b) indicates that all woodcreepers are characterized by muscular specializations that strengthen flexion and weaken extension of the hind limb. The most striking modification of the hindlimb muscles of woodcreepers is that most of the leg tendons are heavily ossified, a pattern otherwise unknown in passerines. These modifications probably relate to a novel biomechanical problem faced by trunk-climbing birds: Whereas a bird on a horizontal substrate uses its hindlimb extensor muscles to counteract gravity, one on a vertical surface must use its flexors to avoid falling away from the tree. Thus, the muscular modifications common to all woodcreepers probably constitute adaptations for climbing. In this instance, phylogenetic analysis has provided insight into derived states of the woodcreeper clade that are important in the use of a novel substrate, the vertical surfaces of trees.

Within the woodcreeper clade, notable modifications in the size and shape of the bill are correlated with differences in feeding behavior, as they are in the Hawaiian honeycreepers, one of the classic examples of adaptive radiation (Raikow 1977). The woodcreepers show a wide array of bills (Figure 6), which are used in a variety of trophic contexts. For example, the two species of *Glyphorhynchus* have unique, dorsoventrally beveled, wedge-shaped bills used for flaking off pieces of tree bark to find insect prey. Alternatively, a short, unbeveled bill, as in *Sittasomus* and others, is used for gleaning prey from surfaces, whereas elongate bills are adapted for probing into crevices (e.g., *Campylorhamphus*) or soil (*Drymornis*). The heavy bills of *Dendrocolaptes* and others are used for tearing into wood in search of insects. Although woodcreeper bill form has not been measured in a quantitative and objective fashion, general inspection suggests that the extent of variation is exceeded by that in, for example, the Hawaiian honeycreepers (Drepanidini), which probably evolved in the near absence of other passerines, unlike the woodcreepers. A more objective comparison deals with muscular variation in the hind limb, which in woodcreepers greatly exceeds that of the Hawaiian honeycreepers (Raikow 1976, 1993) and probably reflects the greater range of substrates used by woodcreepers.

Woodcreeper diversification fits well with the classic, adaptive-zone model of radiation, in which extensive, bill-based trophic niche variety arises within a clade that occupies a distinct, novel environmental setting. However, phylogenetic analysis indicates that not all groups follow this classic model of adaptive radiation, as the following two examples demonstrate.

The New World nine-primaried oscines. One of the most remarkable passerine assemblages consists of the tanagers, cardinals, Neotropical honeycreepers, Hawaiian honeycreepers, New World orioles and blackbirds, and other oscines called, on the basis of a mainly New World distribution and a reduced tenth primary feather on the wing, the New World nine-primaried oscines. Their monophyly was established by Raikow (1978) in an expansion of his 1977 study of Hawaiian honeycreepers. He removed from the assemblage the vireos (Vireonidae), which had long been considered part of the group but which lack its derived muscular characters. Sibley and Ahlquist (1982) independently excluded the vireos based on DNA hybridization comparisons. Bledsoe (1987, 1988) and Sibley and Ahlquist (1990) presented additional DNA hybridization data; although their studies included only a small sample of the roughly 1000 species in the nine-primaried assemblage, they were successful in revising traditional views about its diversification.

The most important finding of these studies was that the traditional subgroupings, such as the tanagers (Thraupidae), finches (Fringillidae), and Neotropical honeycreepers (Coerebidae) of Wetmore (1960), or the New World sparrows (Emberizinae) of Paynter and Storer (1970), are not monophyletic. Instead, members of these traditional groups split into several clades. South and Central American sparrowlike species, such as the Saffron Finch (*Sicalis luteola*) and the Diuca Finch (*Diuca diuca*) group with the tanagers, not with the North American emberizine sparrows, although they are similar in bill structure and trophic habits. Likewise, the "coerebid" honeycreepers do not form a clade; instead, they link separately with several subgroups of tanagers. Other "problem" taxa, such as the Swallow-Tanager (*Tersina viridis*) and the Plush-capped Finch (*Catamblyrhynchus diadema*), also group in the tanager clade. These results challenge the traditional view, summarized by Raikow (1978), that the major subgroups are products of adaptive radiation into discrete adaptive zones defined mainly in terms of feeding specializations. Instead, we see a much more complex and dynamic situation, in which feeding specializations in several lineages have repeatedly converged upon morphological and trophic attributes of other lineages. Furthermore, this process has occurred at several levels of the New World nine-primaried assemblage (Bledsoe 1988). The assemblage as a whole represents a continental radiation similar to that of the Hawaiian honeycreepers, but vastly greater both in species number and anatomical, behavioral, and trophic variety. Many details remain to be determined, in large measure because relatively few species have been studied. But the available evidence is sufficient to support the new model of diversification, in which no obvious trophically related trait characterizes the more diverse subgroups of the radiation.

Australo-Papuan oscines. A similar picture emerges from analysis of the phylogenetic relationships of Australo-Papuan oscines. Sibley and Ahlquist (1990) used DNA hybridization data to identify an unsuspected radiation (the Corvida) composed of primarily Australo-Papuan groups; these groups had been previously linked with Eurasian forms on the basis of similarities now recognized as convergent. The radiation proposed by Sibley and Ahlquist (1990) is vast, both in number of species and variety of bill and other trophically related traits, and its recognition constitutes a major discovery in passerine systematics. The Sibley and Ahlquist proposal has been received favorably by most avian systematists, based primarily, we believe, on the intuitive feeling that led earlier workers to question traditional classifications of endemic Australian oscines. Harder supportive evidence was provided by Christidis and Schodde (1991) in the form of protein comparisons, analyzed as distances both with and without the assumption of a molecular clock and also analyzed cladistically as discrete-character data. These analyses also identified an endemic radiation of Australo-Papuan oscines. Although the details of branching within the radiation differ between studies, the DNA and protein results support the existence of a substantial oscine radiation in the Australo-Papuan region.

The structure of the radiation parallels that of the nine-primaried oscines. Nectarivores, frugivores, flycatchers, gleaning insectivores, and climbing forms are all represented in the Corvida radiation, and no obvious trophically related trait characterizes the subgroups within the radiation. A notable difference is the absence of finch-billed, primarily granivorous species from the Australo-Papuan assemblage. Nonetheless, the similarities are striking and suggest again that the traditional model of diversification of single clades into single adaptive zones is in this instance inappropriate.

Specific uses of passerine phylogeny

The considerations described above deal in general terms with the structure and meaning of phylogenetic information. Yet phylogenies also provide a framework for a more rigorous, explicit approach to assessing evolutionary and ecological hypotheses. Phylogenies can serve as invaluable tools for studies of a wide variety of problems. In this section, we discuss three examples taken from our own work. First, we use the woodcreeper phylogeny discussed above to analyze the role of natural selection in evolutionary reduction and loss. Second, we use the broad pattern of New World nine-primaried songbird phylogeny to examine the hypothesis that DNA sequences evolve in a clocklike fashion. Third, we use avian phylogeny as a whole to examine the possible role of key adaptations in the evolutionary success of the passerine birds.

Evolutionary reduction of woodcreeper tendon ossification. The most striking modification of the hindlimb muscles of woodcreepers is the evolutionary conversion of many leg tendons into ossified, bony rods. This conversion occurs almost exclusively in muscles that flex the leg and the toes. We hypothesize that tendon ossification is an adaptation to prevent stretching of the flexor tendons (Bledsoe et al. 1993, 1997), which, as discussed in the section "Passerine adaptive radiation," are under heavy and prolonged loading during vertical climbing.

To gain insight into the evolution of tendon ossification, we analyzed the phylogenetic pattern of tendon ossification in woodcreepers by mapping the presence or absence of specific tendon ossifications onto the woodcreeper phylogeny (Bledsoe et al. 1993). This mapping revealed that one clade within woodcreepers—the *Dendrocincla* group—is characterized by six inferred losses of tendon ossification. In his anatomical study of woodcreepers, Raikow (1993) dissected two specimens of one of the *Dendrocincla* species. These two specimens differed so markedly from one another in the extent and pattern of tendon ossification (Bledsoe et al. 1993) that the possibility of a correlation between evolutionary reduction and increased within-species variation arose. Subsequent study of larger series of one *Dendrocincla* species and two woodcreepers outside the *Dendrocincla* clade indeed revealed a five- to tenfold increase in intraspecific variation, depending on the measure of variation, within the *Dendrocincla* clade (Bledsoe et al. 1997). Of substantial interest was the additional observation that some of the variations were *gains* of ossification within the *Dendrocincla* clade. We believe that such a result is inconsistent with directional selection for reduction in tendon ossification. Instead, alternate mechanisms, such as the accumulation of selectively neutral alleles that cause variability in developmental expression of ossification, may eventually cause the evolutionary loss of ossification. Only one *Dendrocincla* species has been studied so far, and additional dissection is needed to test this hypothesis.

Nine-primaried oscines and the molecular clock. Since Zuckerkandl and Pauling (1962) proposed the existence of a molecular clock, systematists have been keenly interested in using phylogenies to test the proposition that macromolecular sequences evolve in clocklike fashion, that is, at a constant rate. Sibley and Ahlquist (1990) argued that a molecular clock characterizes the genome-wide evolutionary divergence of DNA sequences in many groups of birds. Although Sibley and Ahlquist never rigorously tested their hypothesis, several ways for doing so become apparent once a phylogenetic reconstruction is obtained.

One method of testing the clock hypothesis involves the use of relative rate tests. If two taxa are closest relatives (sister taxa), and if the single-copy genomes of each have evolved at the same rate, then the distance from either one to a third taxon should be the same. This logic can be extended throughout a branching pattern, making many such tests possible. Because DNA–DNA hybridization data take the form of distances, phylogenies derived from such data permit multiple relative rate tests. For the nine-primaried songbirds, Bledsoe (1988) used nonparametric statistical tests to look for nonrandom variation in distances of sister taxa, which would falsify the clock hypothesis, and found no statistically significant deviation from random variation resulting from measurement error. Such techniques are free from the assumptions of parametric statistical methods but suffer a loss of sensitivity. Consequently, as Bledsoe (1988) showed, rates could vary by as much as 10% without being detected.

Table 3. Characters proposed as passerine key adaptations.

Key adaptation	Category	References
Small body size	Single character	Kochmer and Wagner 1988
Vocal complexity	Single character	Fitzpatrick 1988, Vermeij 1988
Large brain size, advanced capacity for learning, overall behavioral plasticity	Correlated multiple characters	Fitzpatrick 1988
Sexual selection by female choice	Mating system	Barraclough et al. 1995
Flexibility in nest placement	Reproductive strategy	Collias 1997
Arboreality, behavioral flexibility, diurnality, insectivory, and others (see text)	Multiple uncorrelated	Fitzpatrick 1988, Baptista and Trail 1992

A second method, based on parametric statistics, utilizes the degree to which the original, observed distances between species match those distances obtained by measuring path lengths through the phylogeny, which are derived from analysis of the original distances. The better the match, the better the estimate of phylogeny. Bledsoe (1988) ran two analyses, one in which the phylogeny was inferred without assuming a molecular clock and the other in which a clock was assumed. He obtained identical branching patterns and hence could validly compare, using an F test, whether the tree that did not assume the clock had a significantly better fit to the original matrix. Such a result would falsify the clock hypothesis. Using a sum-of-squares measure of fit, he found no significant difference between the "clock" and "no-clock" trees.

Thus, the data suggest that the assumption of a relatively constant molecular clock seems appropriate for the nine-primaried songbirds. Although there are some technical problems with the application of both parametric and nonparametric statistical techniques, the concordance of results is sufficient to indicate fairly clocklike behavior. However, studies of other groups have obtained different results. For example, Sheldon (1987), using an approach similar to the one described above, found significant rate variation in single-copy nuclear DNA evolution in herons. There is substantially more to the clock issue than presented here, but the results of the two studies discussed above are sufficient to illustrate the main point: Phylogenies provide valuable tools for studying such important evolutionary phenomena as the molecular clock.

Passerine diversity and key adaptation. The passerines are unusually species rich compared with other groups of birds. This high diversity has led many researchers to propose specific causal factors that might account for passerine success (Table 3). The underlying concept that unites these proposals is that of key adaptation. The definition of key adaptation varies among biologists, but the central idea is that an adaptation is termed key if, by virtue of possessing it, a given group's members experience either an increase in speciation rate, a decrease in extinction rate, or both. Hence, the adaptation can be considered responsible for the increased species richness of a group compared to other groups. Key adaptation hypotheses are common in the systematic literature on angiosperms, beetles, bats, and many other diverse groups of organisms, including the passerines.

Despite their intuitive appeal, key adaptation hypotheses are controversial for several reasons. First, the possible mechanistic basis for cladewide changes in speciation or extinction rates is often unclear. For example, among the derived characters that support the hypothesis of passerine monophyly (Table 1) and would therefore be potential key adaptations, Raikow (1986) found that none of the characters could be construed as necessary for the success of the group. The derived states consist of minor structural modifications with no plausible link to a change in speciation and extinction rates. The only plausible exception involves the mechanism of the passerine foot, which has three distinctive features: The evolutionary loss of most of the small muscles of the forward toes precludes various subtle movements of the individual digits; an enlarged hind toe provides a balanced grip in conjunction with the three forward toes; and two muscles (flexor digitorum longus and flexor hallucis longus), which flex the forward toes and the hind toe, respectively, are functionally independent because they lack a connection between their tendons. The passerine foot is thus marked by simplicity and economy of structure. In contrast, the mousebirds (Coliiformes) of Africa have a foot of unparalleled complexity (Figure 7). Individual digits can be moved into various positions because the intrinsic musculature is uniquely complex, and the foot is used in a variety of behaviors (Berman and Raikow 1982). Yet the mousebirds have only six extant species. An adaptive scenario can be devised to explain these differences, extolling simplicity and efficiency against the stultifying effects of overspecialization. Nevertheless, if the mousebirds had thousands of species and the passerines only a few, an equally plausible adaptive explanation could be constructed extolling the sophistication and versatility of the mousebird's appendage (Raikow 1986). There is no evidence that the design of the passerine foot provides a convincing explanation for passerine species-richness.

Several key adaptation hypotheses are based on plausible mechanistic connections to increased speciation rates or decreased extinction rates. For example, Mitra et al. (1996) suggested that strong sexual selection, which they measured conservatively by the occurrence of promiscuity, should accelerate evolutionary change in secondary sexual characteristics and hence increase the rate at which allopatric populations speciate. Such proposals are

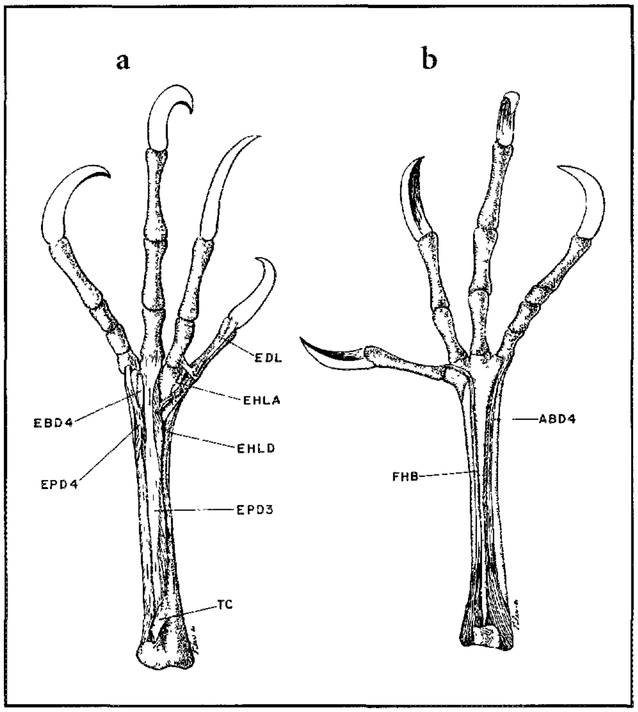

Figure 7. Mousebird (*Colius*) foot. (a) is the dorsal view; (b) is the plantar view. The figure illustrates the complexity of the intrinsic musculature. Labels denote abbreviations of muscle names. Figure reprinted from Berman and Raikow (1982).

advances over key adaptation hypotheses for which researchers have not proposed a mechanistic basis. However, a separate, more basic problem confounds the identification of key adaptations: How, exactly, can key adaptation hypotheses be tested (Raikow 1988)? The best attempts to date involve correlations between the independent evolution of an adaptation in several groups and a high number of species in such groups (e.g., Mitra et al. 1996). However, the number of species in a clade is a group property, not a property of individual species. As such, the comparative approach to key adaptations differs in a fundamental way from other comparative tests in which the occurrence of specific adaptations are themselves contrasted. A related problem is comparability of adaptation. Sheldon and Gill (1996) pointed out that each group is unique with respect to both the putatively comparable adaptation and the ecological and evolutionary histories of the group.

It is important to note that we are not arguing that the number of species in a clade has no antecedent causes—it must, of course. Instead, we argue that identification of a single antecedent cause, or even a combination of causes, has yet to be convincingly made. A related point is that arguments about combinations of causes are themselves problematic. For example, Fitzpatrick (1988) and Collias (1997) favored the view that passerine success must result from some combination of attributes, including arboreality, behavioral flexibility, complex learning, diurnality, large brain size, small body size, insectivory, an early age of first breeding, excellent dispersal abilities, high metabolic rate, short generation time, and vocal sophistication. This approach reduces to the truism that the evolutionary success of a group is somehow related to its attributes. Such a statement is sorely lacking in explanatory power.

Null model explanations of passerine diversity.

The debate about the evolutionary success of the passerines rests on the unstated assumption that passerines are unusually species rich. They appear to be, simply because they make up more than half of Earth's extant avifauna. Yet evolutionary success is a relative concept. The question of why there are so many species of a particular group has little meaning unless one asks "compared to what?" The traditional approach has been to compare the group in question with others of the same taxonomic rank. However, there is no reason to believe that traditional taxa of the same rank are equivalent, in the sense of being clades of the same age. The only such clades that can be identified with certainty are sister groups—two monophyletic groups that are each other's closest relative and hence by definition are of equal age. Comparison among sister groups, therefore, is the answer to the problem of categorical inequivalence (see Raikow 1988).

The question then becomes whether sister groups differ in number of species. Virtually every pair of sister groups will differ in size, however slightly. Hence, the issue is one of degree of imbalance. In 1989, Slowinski and Guyer, recognizing the importance of sister-group comparisons and the issue of degree of imbalance, restated the diversity problem in terms of a null approach, in which one asks whether the difference in diversity between two sister groups can be explained by stochastic processes alone. Using a Markov model in which each species has an equal chance of splitting or going extinct in each generation, Slowinski and Guyer (1989a) demonstrated that "a random branching process *inherently produces sister taxa of disparate size*, thereby emphasizing the need to test the reality of determinism in the evolution of clades" (p. 190; their emphasis). In addition, they (1989b) provided a method by which, for any pair of sister taxa, one may calculate the cumulative probability that the number of species in each sister group, or in an even more asymmetrical pair of values, can be ascribed to chance. We calculated this probability (see box page 497) for the passerines and their sister group, using the phylogeny of Sibley and Ahlquist (1990) and the species numbers (5712 passerines and 1536 of their sister group) of Sibley and Monroe (1990). The value at which we arrived, 0.42, is a high probability by any standard measure and throws into question the very idea that the passerines are an unusually species-rich group. If one accepts the validity of the null model approach and its assumptions, as well as the phylogeny and species numbers used in the analysis, then there is no need to seek a deterministic explanation for the observed diversity. Ironically, the impassioned debates of the past decade

Null model calculations

The null model of diversification introduced by Slowinski and Guyer (1989b) assumed that phylogenetic branching is dichotomous, that lineages cannot merge, and that the probability of speciation and extinction is equal in all lineages. This Markov model yielded the interesting result that a random branching process inherently produces clades that have quite different levels of species richness. They presented the equation shown below to calculate the probability of generating clades of different sizes under the null model. The calculations establish the probability of obtaining observed species numbers in sister groups, which are clades of equal age. The probability of obtaining any specific pair of species numbers is very small. The appropriate probability, therefore, is the probability of obtaining the observed pair of numbers, or an even more asymmetric pair. This cumulative probability can be used to answer the question of whether sister groups have levels of species richness that differ statistically from the expectations of a random branching process.

The phylogeny of Sibley and Ahlquist (1990) hypothesizes that the sister group of the passerines is a clade consisting of members of several avian orders listed by Wetmore (1960), including doves (Columbiformes); cranes, rails, and their allies (Gruiformes); shorebirds, gulls, and allies (Charadriiformes); and several other orders. The species numbers were taken from Sibley and Monroe (1990): passerines (s), 5712 species; sister group of the passerines (r), 1536 species.

$$p(r,s) = 2r/(n - 1) = 2(1536)/(7248 - 1) = 0.42,$$

where

$p(r,s)$ = the probability of obtaining the observed levels of species richness or an even more asymmetric pair of values,
r = number of species in the smaller group,
s = number of species in the larger group, and
$n = r + s$.

This probability value, 0.42, is substantially higher than 0.05, which is typically used as a threshold for statistical significance. Hence, the result indicates that the observed levels of species richness are not significantly different from those expected under the null model. There may be no need to resort to key adaptation explanations when random branching of lineages is all that is needed to explain the observed levels of diversity.

(see the references column in Table 3) may be beside the point: The observed imbalance is not great enough to require anything but a stochastic explanation for the observed species numbers.

The Markov model is not without its problems. Two of its hidden assumptions (Losos and Adler 1995) are of particular concern: that speciation is essentially instantaneous and that speciation events are independent of one another. Violations of these assumptions render the Markov model less sensitive to significant imbalance. Several additional problems come to mind, not the least of which is the validity of the Sibley–Ahlquist sister group of the passerines. This split occurs from a short internode deep within their tree, precisely the kind of situation in which the tree is most likely to be inaccurate (Gill and Sheldon 1991, Lanyon 1992). But even this problem may not be too troublesome, because if one assumes the validity of the Markov null model, then the sister group of the passerines would have to have 146 or fewer species to reach $p < 0.05$. Among nonpasserines, where the sister group of the passerines must lie, most traditional orders (at least some of which are likely to prove monophyletic) either comprise more than 146 species (e.g., Columbiformes) or are unlikely to be the sister group of the passerines (e.g., Procellariiformes).

A final potential problem is biased taxonomic undersplitting. If passerines are more undersplit taxonomically than nonpasserines (among which the sister group of the monophyletic passerines must lie), then a greater imbalance will be predicted than is observed with current species-level classifications. Again, this may not be a severe problem. The trend in the past decade toward recognition of geographically distinct, primarily allopatric forms has led to a slightly larger increase in numbers of passerines than nonpasserines, from 5274 passerines (Bock and Farrand 1980) to 5712 (Sibley and Monroe 1990), and from 3747 nonpasserines (Bock and Farrand 1980) to 3960 (Sibley and Monroe 1990), or increases of 8.3% and 5.7%, respectively. The bias would have to be substantially greater than this to reach significant imbalance, at least under the Markov model.

Future directions

Work to date has been successful in establishing the broad structure of passerine phylogeny, but several critical questions remain to be answered. High among the challenges that lie ahead will be to identify the sister group of the passerines. That information is key for answering questions about passerine origins and about whether passerines really are more species rich than expected under the null model approach.

Another area that holds substantial promise is the detailed analysis of the large oscine radiations. We have successfully established important generalizations about the ecological structure of these radiations. However, more detailed estimates of phylogeny for groups such as the Australo-Papuan oscines are needed for gaining insight into, for example, the circumstances of origin of cooperative breeding, which is unusually common among the Australo-Papuan songbirds.

Finally, substantial uncertainty surrounds the details of relationships among the New World suboscines. In particular, the relationships among antbirds, and between antbird groups and other members of the Furnarii, are unclear. Each major group in the Furnarii is highly distinctive myologically, but establishment of homologies between characters of the different groups has so far proved difficult. Other sources of data will be needed to augment the myological information. Nonetheless, if studies of the past two decades are any indication, the future holds promise for continued, important insight into passerine biology and ecology through application of the comparative approach.

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