Future Challenges of Systematic Ornithology*

Ernst Mayr**

On the occasion of the centennial of the American Ornithologists Union I remarked: "A science is like a tree. It is forever growing and reaching out in all directions. New branches develop, but some earlier branches may stop growing, being shaded out by the new branches. However, there is one aspect in which science seems to differ from a tree: the older it gets, the more vigorous its growth seems to be. This is certainly true for ornithology" (Mayr 1983).

This observation leads us to the questions which are at the present time the most vigorous branches of the tree of ornithology, and where might one expect new branches to sprout? Perhaps the safest way to make predictions is to extrapolate from past developments. When one looks back over the past 25 years one can observe some definite trends in the development of ornithology. A study of the contents of the ornithological journals in all countries shows that straight description is increasingly supplemented by causal analysis. Furthermore, more and more of the publications are authored by ornithologists whom one can designate as professional biologists, that is, professors at universities, curators in museums, and researchers in scientific institutions. There are still some superb amateurs, but they now represent a minority. A consequence of this development has been the integration of ornithology into biology. The major problems of modern ornithology are also the problems of ecology, behavioral biology, systematics, and evolutionary biology. The formerly existing barriers between these fields and ornithology have largely disappeared.

The contributions made by ornithology are so important for some of these fields because the knowledge of the taxonomy of birds is so mature. Almost all species of birds from all parts of the world are by now known, their geographic ranges have been well established, and we have detailed life history observations for a large percentage of them. This splendid factual foundation permits the establishment of more secure inferences from birds than from any other group of organisms. Yet this rich treasure of factual knowledge has been exploited so far only very incompletely and it will be my task to indicate how this wealth of information can be exploited in future researches.

Before getting into detail, let me mention also that ornithology has not only made important factual contributions but has been a major influence in the shaping of the conceptual structure of biology. In particular, ornithologists can claim an important share in the development of three major basic concepts in biology. First, the development of population thinking, which has played such an important role in evolutionary biology, secondly the recognition of the dual causation of all biological phenomena
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(proximate or physiological, and ultimate or evolutionary causations), and third, the realization that observation is of equal importance as a tool of scientific investigation as the experiment.

**Evolutionary Biology**

Birds, for the above stated reasons, have been a major source of information for evolutionary studies, from Darwin's days to the present. It was the geographic variation of the mockingbird on the Galapagos Islands that convinced Darwin of the occurrence of speciation, and birds furnished Darwin with more evidence of sexual selection than all other groups of organisms together. Indeed, there is hardly a branch of evolutionary biology to which birds have not made a contribution. Ornithology has contributed equally to the two great branches of evolutionary biology, the study of organic diversity and the study of adaptation.

Let me begin with the study of diversity. No other aspect of the living world is as spectacular as its diversity. Even though birds are only a minute part of this enormous diversity, about 9,000 species among the millions of kinds of organisms, the study of birds has been foremost in contributing to our understanding of this diversity. Even at the purely descriptive level birds are better known than any other group of organisms. Ninety-eight per cent of all the species of birds in the world had already been described 50 years ago. They had not only been described but for most of these species the geographic ranges had been outlined in great detail, and much had been learned about their life histories. It was this intimate knowledge of the diversity of birds which enabled ornithologists to become the leaders in the new systematics. It was ornithologists who were in the front line of solving the problem of the multiplication of species and of clarifying the nature of species. And this permitted ornithologists to show through the study of the components of superspecies what an important role speciation plays in macroevolution.

But what about the future? Where will be the further developments in avian systematics? Here we encounter a remarkable discrepancy. Systematics has two branches, microtaxonomy and macrotaxonomy. There is no other group of organisms in which microtaxonomy, that is, taxonomy at the level of the species, is further advanced than ornithology. And yet macrotaxonomy, the classification of birds, had lagged far behind until the last 15 or 20 years.

**Microtaxonomy**

Although two or three new species of birds are still being discovered annually, mostly in South America, the inventory-taking of the species of birds has virtually been completed. More importantly, the population structure of most geographically variable species has been carefully analyzed, leading to the recognition of numerous polytypic species. There is still some indecision whether certain geographically isolated subspecies should or should not be raised to the rank of allospecies, but this is not really a
科学问题而不仅仅是惯例。

地理代表性的物种，在许多地区，特别是北美和巴布亚新几内亚地区，已经被一致地合并成超物种（由亚物种组成）。这种超物种的识别对于两个原因都很重要。首先，它记录了一种有趣的物种形成阶段，几乎完美地展示了物种形成的地理过程。其次，将地理代表性的物种合并成超物种对动物地理学家来说很重要，因为超物种在任何地方只由单个亚物种代表。正如伦施敏锐地指出，当我们编制不同部分世界动植物区系的目录时，我们必须计算超物种而不是亚物种，以免误导。伦施的地理物种是由两个元素组成的：孤立的物种（不是超物种的成员）和超物种。到目前为止，还没有尝试对鸟类的全部地理物种进行一致的列举。

**亚种**

从20世纪20年代到40年代，描述新亚种是鸟类分类学家的主要工作。亚种被分得越来越细，一位作者甚至建议人们只在北光下，将标本放在中性灰色的纸上进行比较，以便能够感知到两个系列之间的最小差异。在这一时期，我自己也命名了一些亚种，例如在新赫布里底群岛的Pachycephala pectoralis种群，今天我不会再考虑重新认识它们。诚然，它们是可以区别的，但命名这些种群为亚种不仅没有揭示出这些稍微不同的种群之间的真正差异，而且没有揭示出更明显的亚种。现在普遍认为部分种群是很少值得重新命名的。事实上，从最近的文献来看，我现在有一种印象，认为以前被命名的亚种比新被描述的亚种要多。这并不意味着不应该仔细描述地理变种的趋势，但意味着只有那些明显不同的种群才应该被命名为亚种。

**种**

鸟类学，在过去的100年里，已经从识别严格分类的种到识别多型种的转变。这一转变在很大程度上是形式化的，是一种方便的分类方法，即识别出名义种。现在做了很少的进化分析多型种。如果我们在岛上研究多型种，并首先只研究岛上的物种，我们会发现每个主要岛屿都有不同的亚种或亚种。每个亚种或多或少地孤立，代表一个即将产生的新物种。在大陆上，多型种往往有几乎未被打破的广泛分布，并以一种严格的一般性表现出地理变种。这意味着这些是或多或少孤立的，代表一个新的特例。这种情况下，应该描述的亚种是那些在其特性上是明显不同的亚种。
tics by the local environment, and neighboring populations are adapted to the environ-
ment of the adjacent area. However, in addition to such clinally varying species of
continuous distribution, there are others, which consist of isolates, even though distrib-
uted on continents. This has been excellently illustrated by Keast in his study of specia-
tion in Australian birds (Keast 1961). Most of these isolates occur beyond the periphery
of the contiguous populations in the center of the species range. It is quite evident,
however, that such isolated species populations expand during favorable climatic periods,
but contract into refuges during unfavorable periods. Such a history has been de-
monstrated particularly convincingly by Haffer for the species of birds of the Amazonian
region. If the isolation in the refuges was only temporary and the isolates had not yet
acquired isolating mechanisms, populations during the subsequent period of species
expansion will sooner or later encounter other expanding isolates or else the parental
species population. A belt of secondary hybridization will then be established in the
zone of contact. Recent researches in Eurasia, Africa, South America and North
America have shown that almost all more pronounced subspecies of continental species
are ex-isolates and meet with other subspecies of the species in a rather sharp zone of
intergradation.

What is needed now is a more systematic analysis of the population structure of
all species of birds. What proportion of species are monotypic? How many species
are polytypic? How many polytypic species vary only clinally? Which others have
peripherally isolated subspecies? And which contiguous species have subspecies that are ex-isolates? Such a statistical analysis is particularly important for
evolutionary explanations. Is it true, as has been suggested, that all new species originate
by peripatric speciation, that is by the genetic restructuring of peripherally isolated
populations? Or could contiguous subspecies diverge increasingly until finally they
become good species by parapatric speciation? Mayr and O'Hara (1986) have analyzed
one set of cases attributed to parapatric speciation and were able to refute this hy-
pothesis. The actual distribution pattern was entirely consistent with the theory of
peripatric speciation.

Genus. The role of the genus in ornithological classification is well established.
The time is far behind us when authors like Oberholser and Mathews placed just about
every species in a different genus. We now know that it is the role of the genus to
bring together groups of species sharing common descent and sharing derived characters.
Perhaps in ornithology we still recognize too many genera, a little over 2000, for the
9041 species of birds. However, since the generic name in the system of Linnaean
nomenclature is part of the scientific name of a species, there is the danger of loss of
information when the lumping of two genera leads to a change in the scientific names
of some of the included species. Personally I consider it a step in the wrong direction
when a few cladists have recently tended to place in a different genus every species that
has a unique derived character. There are of course many species that are so distinct
that there is no question about the justification of their generic separation even though
they are the only species in their genus. On the other hand, to bring out finer distinc-
tions is the role of the species and not that of the genus.
Macrotaxonomy

This branch of systematics deals with the classification of the species of birds into the higher taxa of the Linnaean hierarchy of categories. As progressive as ornithology was in microtaxonomy, as backward it was in macrotaxonomy. In contrast with mammals or insects or other groups of animals, birds are morphologically remarkably uniform. Furthermore, the characters traditionally used to characterize the genera and families of birds, such as the structure of the bill or the feet, are adaptations for particular ecological niches and, as has become quite clear, may have been acquired independently many times by unrelated groups of birds. There are unrelated flycatchers, warblers, shrike-like and finch-like birds in Eurasia, America, Africa and Australia. Auks and penguins, loons and grebes, long-legged wading birds like storks, herons and flamingoes, and many other such ecological analogues are not at all as closely related as was suspected by the early avian classifiers. But what other characters are there that might be useful for the avian taxonomist? Many morphological characters were tried, but the results were so unsatisfactory that Stresemann, 200 years after Linnaeus, despaired that we would ever be able to determine the relationships of the higher taxa of birds (1959: 277). Fortunately the situation has entirely changed in the last 30 years. A group of avian anatomists, including Bock, Homberger, Houde, Lanyon, Olson, Peters, Raikow, and several others, has shown that there are previously overlooked morphological characters and that their proper application sheds a good deal of light on relationships, particularly within orders and families.

More importantly, in this recent period an entirely new set of taxonomic characters was discovered. I am referring to molecular characters. These characters have two great advantages. First, they are an enormously rich reservoir of information, since each molecule has its own evolutionary history. Secondly, each set of molecules is independent of all the others. Hence, the information gained let us say from DNA hybridization can be checked against information derived from other molecular characters, such as mitochondrial DNA or ribosomal RNA. Furthermore amino acid distributions and alleles of enzyme genes can be used, in fact have already been used with great success.

The most comprehensive and indeed heroic endeavor in this new area is Sibley's work on DNA hybridization. He compared the DNAs of more than 1000 species and proposed a new classification of birds based on the degree of similarity of the DNA of the investigated species. Professor Sibley has told me that he does not consider his proposed classification to be the last word, and I have pointed out in a commentary (Mayr 1989) why this preliminary system still has weaknesses. Nevertheless, it must be emphasized that Sibley has established an entirely new foundation, or, as Popper would say, a large set of new conjectures that can now be tested by other methods, morphological or molecular, and either be confirmed or refuted. There is little doubt that the testing and improving of previously proposed classifications is now the most challenging and exciting task of the avian taxonomists.

The becoming available of this rich array of new taxonomic characters happened
to coincide with a controversy in the field of taxonomy, as to the best philosophy of taxonomy. This is not the place to enter this controversy, but it must be mentioned that there are now authors who think that a genealogy is all that is needed for classification, while more traditional ornithologists believe that there are certain basic principles of classification, such as a desirable amount of homogeneity of taxa, which a genealogy can not provide. Up to this point this has not been a major practical problem in ornithology.

The adoption of molecular characters in ornithological research has resulted in a notable revolution in methodology. Previously all an ornithologist needed for his research were skin collections and anatomical specimens. These were stored and studied in museums. The use of molecular characters, however, requires experimental laboratories. Most major museums, realizing this necessity, have now developed such laboratories. Furthermore, since DNA investigations and electrophoresis studies can be done by anybody with laboratory facilities, molecular studies of birds have now been taken up in many university laboratories that have no connections with any museum. This, one can hope, will lead to a considerable broadening of the basis of molecular research on birds. A student in one of these laboratories can select a very limited problem, let us say the relationship of loons and grebes, or of falcons and the other birds of prey, or of the Rheidae and Tinamidae (in relation to Struthio), without the need for a broad-based collection. As soon as the results of such studies have been published they become available for comparative studies.

I have heard one student ask, do we still need to do morphological research in view of the spectacular achievements of molecular taxonomy? The answer is clearly yes. By this I do not mean that the molecular findings necessarily need to be confirmed by morphology, because there are numerous molecular methods that can confirm or refute each other. My yes is meant in a very different sense. Let me explain.

The latest findings of molecular taxonomy usually confirmed what we had believed all along. However, there are spectacular exceptions. For instance, Sibley's demonstration that nearly all endemic Australian Oscines (songbirds) are more closely related to each other than they are to their ecological analogues in the Holarctic, was rather unexpected. This means that the flycatchers, warblers, nut-hatches, tree-creepers, shrikes, nectar-feeders, etc. of the two continents are convergent developments, starting from entirely different ancestries. Hence their similarity ought to be only superficial, and a more careful analysis of their morphology should show how much the originally different structures had to be modified to permit the filling of the new niche. The major Fragestellung is no longer the search for the common ancestor, but the elucidation of the compromise between the ancestral structure and the new functional demands.

One could even go one step further. The remodeling of each analogue produced a number of characters that are clearly adapted but other structural changes may well be chance developments. They might have been merely byproducts of the evolutionary change without having been specially selected. I happen to be a great believer in the so-called adaptationist program of research, which considers characteristics of animals not merely as godgiven helps for the taxonomist. I ask therefore about each charac-
teristic what its function might be and whether it had received its form as a result of ad hoc selection or, as it is usually called, "by chance", that is by stochastic processes. There have been a number of valuable functional—morphological studies in birds in recent years, but I feel that the analysis of niche shifts could be carried further. In particular, the careful comparison of taxa that had experienced convergent evolution has so far been rather neglected. I think such comparative functional studies promise to produce rich results.

A different and far more difficult problem is posed by so-called mosaic evolution. This term refers to the uneven rate of evolution of different character complexes. That very different rates occur has been made clear by a comparison of the rates of molecular and of morphological evolution. For instance, the barbets (Capitonidae) of Asia, Africa and South America have always been considered a reasonably homogeneous group. Sibley's work on DNA hybridization, however, has shown that the American branch separated quite early from the Old World branch, and that one subdivision of the American branch evolved into the strikingly different toucans (Ramphastidae). Such differences in the rates of morphological and molecular are very common. Sometimes it seems that it is the morphological characters which evolve rapidly, as seems to be among the 17 groups of birds which Sibley combines in his family of Corvidae. In other cases, the morphology of what seems to be a natural group is rather uniform, and yet on the basis of the strong divergence of the DNA characters, Sibley places part of this group in different higher taxa. Examples are the hoopoes, which Sibley splits into several families, the trogons, which he splits into several subfamilies, and the kingfishers, in which he recognizes three parvorders. No one has yet attempted to explain these discrepancies between morphological and molecular characters. Why are starlings (Sturnidae) and mockingbirds (Mimidae) so similar in their DNA and yet so different in their morphology? Why are the molecular differences between gulls and auks so small, when morphologically the two kinds of birds are so different? How complete a reorganization of the morphology is necessary when a group of birds enters a different adaptive zone? And how little of a reorganization of its molecules does such a shift necessitate? We simply do not yet have the information to answer such questions. However, we will never look for such information unless we ask these questions. The answers can only be found by comparative research, by comparing different molecular systems, and by comparing total morphologies. This involves exploring a great deal of unknown territory. This is of course a part of the old problem why certain evolutionary lineages evolve so rapidly while others seem to experience almost complete stasis. The rapidly improving fossil record of birds may soon permit us to decide which avian taxa are old and seemingly more or less static, and which others are rapidly evolving. From there, unfortunately, it is still a long way to the solution of the question why these taxa differ in their evolutionary rates.

Related to this problem is the other one of successful and unsuccessful families. I call a family successful if it has speciated copiously, has achieved a wide geographical range, and has filled many different niches. I call a family unsuccessful if it has only a single or at best a few species, often of restricted geographic range. One may ques-
tion, however, whether the term successful is the best way to describe richness in species. Is not the osprey (*Pandion*) very successful, by having achieved an almost cosmopolitan distribution? And yet this species is the only representative of a whole subfamily. On the other hand it can hardly be questioned that the Passeriformes are the most successful of all avian orders, with over 5000 of the 9000 species of birds. Until recently, to many evolutionists the phenomenon of species richness would not have posed a scientific problem. However, through the researches of the last 50 years, it has become quite evident that there is a relationship between speciation and macroevolution and this considerably raises the evolutionary importance of speciation. There can be no adaptive radiation unless a taxon, and the species of which it is composed, has the capacity for speciation. This capacity, in turn, depends on a combination of dispersal facility and the capacity to establish permanent founder populations that eventually can turn into new species. A panmictic species of birds, when it is cosmopolitan, can not speciate because it lacks the capacity for the establishment of peripherally isolated populations. It is evident from this consideration that the population structure of species is of considerable evolutionary importance.

**Birds and Zoogeography**

Our virtually complete knowledge of the geographic distribution of birds permits us to test zoogeographic theories statistically. It is now quite clear that the distribution pattern of organisms is to a large extent determined by their dispersal capacities. Mammals, as Darwin already pointed out, have exceedingly low dispersal facilities and (except for bats) virtually never occur on islands that had not been in contact with a continent. Birds, by contrast, can cross water gaps rather easily, and have developed rich radiations on islands such as the Hawaiian islands, the Galapagos and the Antilles. Yet even among birds there are some species that disperse readily and others that do not. Diamond showed that 40 per cent of the 321 lowland species of birds of New Guinea have been unable to colonize any of the numerous islands around New Guinea more than five miles distant from the mainland. Other birds are known to have made colonization flights of more than 1000 miles to New Zealand and to the islands of Polynesia. Indeed, Diamond was able to distinguish five dispersal classes among the birds of the New Guinea Island Region (Diamond 1975). The ease with which some species of birds can cross water gaps is responsible for the fact that most avian distributions can be explained with a minimal reference to the former geological history of the region, quite in contrast with mammalian distributions.

When continental drift was accepted as a valid theory of earth history, in the wake of the establishment of the theory of plate tectonics, everyone expected that this might necessitate a complete rewriting of zoogeography. In particular, it was expected that it would lead to a complete reevaluation of the bird fauna of Australia, a continent now clearly recognized as part of an old South American—Antarctic—Australian plate, the so-called Gondwana land. However, a thorough analysis of the species of Australian birds established that at best fewer than 3 per cent of the birds are related to neotropical elements, while all the rest must have come into Australia through steppingstones from
Southeast Asia (Mayr 1989). To be sure, Australia at an earlier time must have had a Gondwana bird fauna, but owing to circumstances that are not yet fully explained, this older fauna became almost completely extinct, and was replaced during the second half of the Tertiary by immigrants from Asia. This explanation could not have been made without the greatly improved understanding of the relationship of the families of Australian Oscines, made possible through the researches of Sibley and Ahlquist.

The fossil record of birds up to recent years has been rather scanty and poorly studied. This has begun to change. Better methods for the search of small and fragile bird bones, and quite simply the search for bird fossils, has produced numerous, and quite a few rather unexpected, discoveries, such as the widespread occurrence of palaeognaths in America and Eurasia. So far, nothing is known about the avian fossil history in Africa, and little about that of South America and Antarctica. Palaeonto-

**Speciation and Ecology**

Perhaps the most promising area of research for an avian taxonomist is the border-

line area between systematics and ecology. This field owes its origin to David Lack through his classical study of Darwin's Finches (1947). The problem really consists of two sets of questions. The first set concerns the nature of the differences among populations of the same species. When a species establishes a new population in a different area, particularly on a different island, how does the new population react to the change in its environment? To what extent is it able to switch into a new niche or entirely new adaptive zone? How does this affect its evolutionary potential? The second set of problems concerns the ecological interactions of different species coexisting in the same area. Since Lack's pioneering study there have been numerous analyses of the mutual impact of potentially competing species. Such researches can focus on different aspects. Grant and his associates, studying the Galapagos finches, have concentrated on the interaction of species and the effect of climatic fluctuations on the relative well being of either one or the other species. They have provided overwhelming evidence for the power of natural selection. J. Diamond, on the other hand, has concentrated on the effect of potential competition on the pattern of distribution of closely related species (1975). He investigated a narrowly circumscribed area (New Guinea and Northern Melanesia), but there is a great need of analogous researches devoted to other parts of the world. One might think that it is no longer necessary to produce evidence for the effectiveness of natural selection, but the truth of the matter is that there are still doubters, and furthermore certain distributions as well as adaptations remain unexplained until they are made the subject of a specific analysis.

The recent studies have highlighted the conclusion that a good ornithologist must be a good naturalist. Natural populations are simultaneously affected by so many factors of the environment, that their effect can be determined only by long term studies. Changes in weather, vegetation, pathogens, predators, competitors, they all affect the
well being of a population, and it requires many years of study and census work to determine the relative importance of each of these factors. Exemplary for such studies is the work of Woolfenden, Fitzpatrick, and their associates on the Florida Jay, carried out at the Archbold Biological Station, Lake Placid, Florida. Other examples are the work of Peter Grant and associates on the Galapagos Finches, and the work of various ornithologists on Barro Colorado, Panama, under the auspices of the Smithsonian Tropical Research Institute. Happily, similar long term studies are carried out in many countries, at various biological stations, for instance England (Edward Grey Institute), Holland, Germany, Finland, and California. The important lesson learned from these studies of one specific population is that no year is quite like the others. And almost all populations experience sooner or later some sort of natural disaster, such as the El Niño in the Galapagos, a devastating virus epidemic among the Florida Jay, or the appearance of an efficient new predator at the Whytham Woods near Oxford.

Natural populations and species are the arenas of evolution. Recent researches in ornithology have shown that major advances in systematics are made in many different ways, by new techniques, like DNA hybridization, or new discoveries, as avian fossils. It is equally important, however, to ask new questions and to advance new hypotheses, in order to exploit the newly acquired factual information. And as always in the history of ornithology, there has to be a continuing going back and forth between the laboratory (museum) and the outdoors. This is how new ideas originate, and this is how they can be tested. Throughout the history of biology, ornithology has played a leading role in making new discoveries and in developing new concepts. The spectacular achievements of ornithology in the recent past give me confidence to predict that ornithology will continue to play its leadership role in biology.

**Literature**


鳥類系統分類学の未来像

鳥類系統分類学の未来像は多くの分野に存在する。多型種 polytypic species の個体群構造に関するより正確な情報が必要である。それは、どの亜種と亜種が亜種間的に互に移行し、またどの亜種が狭い地理的領域で合っているか、そしてどれが十分隔離されているかなどである。種のうちどの位置割合が単型種 monotypic であるか。これらの違いがそれらの種の生態で説明されるだろうか。それに答えるものとして、いまのところ分子形質（核 DNA, ミトコンドリア DNA, 酵素遺伝子など）の膨大な情報量の利用が始まったばかりである。これらの形質は、現在認められているよりも遙かに良い鳥類の分類を構成するために必要な情報を提供してくれるだろう。これにより新しい形態的形態的学的成研究が可能になる。それは、種が類似性を得た過程や原始構造どのように補償が成立ったかを、見いだすという生態学的相似性 "ecological analogues" の比較である。何故にある鳥類の科や目は種が多く、その他では少ないかを結論づけるには、このように生態学的分析が必要なのである。また、化石学はとくに等関係される分野であり、鳥類の化石を発見するには新しい方法が必要であろう。化石は鳥類の類縁系統やその分布に関する疑問に答えるため緊急に必要だからである。博物館での研究も、将来、種ごとの個体群の長期研究によって補足せねばならない。（黒田長久訳）

Ernst Mayr: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 U.S.A.