Phylogeny and Classification of Passerine Birds, Passeriformes

V. A. Payevsky

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia
e-mail: payevsky@yandex.ru

Abstract—The paper presents an overview of the current state of studying the phylogeny and evolution of the largest taxonomic group of birds—the order Passeriformes. Phylogenetic relationships and problems of the classification of passerines according to the data of morphological and molecular studies are discussed. All the results on this issue obtained during the past 25 years are considered and summarized.

Keywords: Passeriformes, passerines, diversification, classification, molecular studies, phylogeny, evolution

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INTRODUCTION

Among all the existing organisms, the class of birds is one of the most studied. Nevertheless, their origin, phylogeny, and biogeography are the subject of enduring and heated debates, which have significantly multiplied due to the use of molecular data. In our time, birds become a model for the development of the methodology in studying animal phylogeny (Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999; Cracraft, 2001; Kurochkin, 2006).

The greatest diversity among currently living birds belongs to the order of passerine birds, or Passeriformes. This order consists of about 5740 species, or 59% of all living species of birds, that is, of 9672 species in 2057 genera (Sibley and Monroe, 1990). Variable in structure, ecology, and behavior, passerines widely inhabit all terrestrial biotopes on all continents except the Antarctica ices. Passerines are so numerous, both in terms of the number of species and the number of populations in nature, that ornithologists in their daily work usually divide all the birds into passerine and non-passerines.

Most passerines are birds of a small size. The smallest of them, weighing 4–6 g, are the Goldcrest (*Regulus regulus*), the American Bushtit (*Psaltriparus minimus*), and some sunbirds (genus *Cinnyris*), the largest, weighing up to 1.5 kg, are the Common Raven (*Corvus corax*) and Lyrebird (*Menura superba*). They feed mainly on insects, spiders, annelids, seeds, fruit, and nectar. The species associated with forests and bushes dominate; they are the most numerous and diverse in tropical forests. Because of their vast diversity, relative ease of observation, and field studies, including collecting, passerines have long attracted the attention of a wide range of biologists, from taxonomists and evolutionists to ecologists to experimenters.

In 1986, the American ornithologist Raikow (1986) published an article with the stimulating title, "Why are there so many kinds of passerine birds?" The article evoked numerous responses, and soon the issues of phylogeny and evolution of passerine birds become very popular among ornithologists. And because of the rapid advances in the molecular research methods, as well as the intensive development in the paleobiogeographical bird research, many publications on the subject of their origin, adaptive radiation, and diversification rate have appeared. Such an intensification of study over the past 25 years has led to new ideas and a radical revision of the traditional views on the evolution of birds, including passerines. The purpose of this publication is to lead a review of the milestones and results from the study of evolution, phylogeny, and classification of passerine birds.

HISTORICAL MILESTONES OF PASSERINE CLASSIFICATION BEFORE MOLECULAR RESEARCH

Morphologically, passerines are a very homogeneous group, and historically it was assumed that passerines are a monophyletic group. Now their monophyly is well established, both on morphological (Raikow, 1986) and molecular basis (Sibley and Ahlquist, 1990). Nevertheless, the monophyly of passerines is a hypothesis, like many other hypotheses of phylogeny. The key point of progress in the systematics in recent years was the awareness of the importance of the tested monophyletic hypotheses (Raikow and Bledsoe, 2000). Inside the order of passerines, the phylogenetic relationships are very confusing, because most of the evolutionary lineages occurred through very rapid radiation during the Paleogene. As a result of the rapid diversification, there was no possibility of acquiring synapomorphies, which led to unclear delineated groups that complicate the reconstruction of phylogeny (Lanyon, 1988; Feduccia, 1995).

The attempts to construct a classification of birds based only on certain external traits of the body structure, such as the shape of the bill and other obvious morphological differences (Gray, 1869−1871), did not lead to significant advances in the taxonomy of birds, including passerines. Among passerines, there are many unrelated but morphologically very similar ecotypes on different continents, evolved through convergence, as well as species that are related but completely dissimilar in appearance. This fact has always made it difficult to construct a natural system. In the tenth edition of the *Systema Naturae* of Linnaeus (1758), the class of birds already has the order of passerines (Ordo Passeres), although it also lists doves (genus *Columba*) and nightjars (genus *Caprimulgus*), and some passerines are attributed to other orders: genera *Corvus*, *Sitta*, and *Certhia*—to woodpeckers (Picae), as well as shrikes (Laniidae)—to Accipitres (Sibley and Ahlquist, 1990). A detailed chronological overview of the classification of passerines (Sibley, 1970; Sibley and Ahlquist, 1990) clearly showed the difficulties of previous taxonomists in determining the boundaries of the passerine families. The authors of the 19th century classical works on the taxonomy of birds (Fürbringer, 1888; Gadow, 1893) were misled by the morphological similarity within the order, especially among passerine songbirds, forcing them to consider most passerines as closely related species. One can regard a gradual increase in the number of families of passerines in the taxonomical works as a characteristic reflection of overcoming such an approach. Fürbringer (1888) distinguished only two passerine families, but its number in the works of the subsequent authors was: 35 (Gadow, 1893), 50 (Mayr and Amadon, 1951), 60 (Sharpe, 1901−1909), 63 (Stresemann, 1934), 70 (Wetmore, 1960), 72 (Kartashev, 1974), 96 (Dickinson, 2003), and 104 families (Wolters, 1975−1982).

The division of passerines into groups of songbirds, or oscines (or suborder Passeri), and suboscines (Clamatores, or suborder Tyranni) began in the late 19th century (Sharpe, 1877−1890; Gadow, 1893). The species diversity in oscines is much more than that of suboscines; oscines make up almost half of all modern species in the class of birds and represent the largest radiation of birds. These two groups, considered most often as suborders, differ morphologically, primarily in terms of structural features of the syrinx, the vocal organ located at the base of a trachea, at the spot of its divergence into bronchi. The presence or absence of specific internal muscles and cartilages and their location characterizes different types of syringes. In oscines, the syrinx has a complex morphological structure, which provides their complex vocalization, while in suboscines it has a less developed structure, leading to simple vocalization. In addition, all suboscines, unlike oscines, are characterized by a bulbar form of the middle ear bone (Ames, 1971; Raikow and Bledsoe, 2000).

The classifications of birds in the 20th century were predominantly based on the classical works of Fürbringer (1888) and Gadow (1893), many provisions of which, based on reasoning about phylogenetic relationships between taxa, have survived to the present day. In the classification of birds by Sharpe (1901−1909), two groups of passerines—broadbills (Eurylaimi) and lyrebirds, or primitive passerines (Menurae)—were elevated to the rank of orders, along with the order of the rest of passerines. The latter was divided into two suborders: Mesomyodi, with 12 families, and Acromyodi, with 48 families. In the system of birds by Wetmore, since 1930 (the latest edition: Wetmore, 1960), whose classification has been acknowledged by many ornithologists and still continues to be widely used, all Passeriformes were divided into four suborders: broadbills; lyrebirds, or primitive passerines; Tyranni; and oscines (Passeres). The same division was accepted in the subsequently proposed system (Mayr and Amadon, 1951), although in the suborder of oscines the number of families was changed significantly. Thus, the Old World flycatchers (Muscicapidae), for example, besides flycatchers, also included Sylviidae, thrushes (Turdidae), bubblers (Timaliidae), wrens (Troglodytidae), and dippers (Cinclidae). Subsequently, as a result of many studies (Olson, 1971; Sibley, 1974; Feduccia, 1975; Raikow, 1987, etc.), lyrebirds in terms of a number of morphological features were found to belong to songbirds (Oscines), and broadbills and Tyranni were combined into the suborder of Suboscines, although broadbills differ from the rest of suboscines by significant morphological features.

The Wetmore classification was used by Peters in the *List of Birds of the World*, but in the last volumes devoted to passerines (Peters, 1951−1986) the sequence of the Wetmore families was replaced by the so-called Basel Sequence adopted at the 11th International Ornithological Congress in 1954. This list represents passerines as 38 families, among which the family of flycatchers also included, like in Mayr and Amadon (1951), all Sylviidae, Turdidae, and Timaliidae, and the family of buntings (Emberizidae) included, besides buntings, cardinals (Pyrrhuloxiinae) and tanagers (Thraupidae). This sequence of the passerine families (Mayr and Greenway, 1956) begins with larks (Alaudidae) and swallows (Hirundinidae) and ends with birds-of-paradise (Paradisaeidae) and corvids (Corvidae).

The Basel Sequence did not satisfy everyone, and many ornithologists have continued to use the Wetmore system. Of course, the sequence of taxa in any classification can hardly speak about real relations between the groups in terms of time and kinship, so the order of the listing reflects not so much the passerine phylogeny as the convenience for ornithologists. However, the pessimism expressed by Stresemann (1959) that the true phylogeny, and the classification that reflects it, is impossible in principle did not stop

the intensive research of the evolution and systematics of birds.

In the first attempt of a phylogenetic classification of the higher taxa of birds (Cracraft, 1981), the entire class of birds was represented by 20 orders in 9 sections. In the last, the ninth section consisted of four orders—Passeriformes, Coraciiformes, Coliiformes, and Piciformes. The proximity of Passeriformes with Piciformes and Coraciiformes, as was shown by further research (including in terms of the molecular data), was fully reasoned.

In the 1960s−1970s there began studies of the phylogeny of birds according to features of the distribution of proteins in eggs using electrophoresis. The results concerning passerines (Sibley, 1970) showed with some probability, in particular, that: (1) corvids and shrikes (Laniidae) are related, (2) the genera *Psaltriparus* and *Aegithalos* are closely related and are closer to Sylviidae than to tits (Paridae), (3) the families Sylviidae and Muscicapidae are closely related and are quite close to family of thrushes, (4) the family of sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) differ sharply and are not related, (5) the genus of true sparrows (*Passer*) differs from the family of weavers (Ploceidae) and may be closer to finches (Fringillidae), (6) the genus of finches (*Fringilla*) is closely related to the subfamily of cardueline finches (Carduelinae).

PHYLOGENY AND CLASSIFICATION OF PASSERINES BY DNA HYBRIDIZATION

Prior to the 1980s, basic research of the phylogeny of birds was based only on morphological traits. Due to advances in molecular biology and research techniques, the first attempts using molecular methods for solving problems in the systematics of birds had already been taken in 1960s−1970s, and the first significant results on DNA hybridization were published only in the early 1980s (Sibley and Ahlquist, 1983, 1985).

A large-scale phylogenetic picture of the evolution of birds, the first in the history of taxonomy, appeared in the fundamental book of Sibley and Ahlquist (1990). Based on molecular data, it shows the results of the work of numerous researchers on hybridization of the DNA from 1700 bird species from 168 families, where the DNA of each species was crossed in a series with DNA from 25 other species. In general, the data on 24000 hybridizations used for constructing the phylogeny of all birds were obtained. The authors argued that the true phylogeny can only be established through DNA hybridization, where the degree of relationships is expressed through the temperature gradient during hybridization. When constructing phylogenetic schemes, the authors took the main provisions of cladistics (Hennig, 1966), particularly the provisions that the rank of the category should be based on the time of its origin and that sister groups should be

assigned with the same rank. The principles of the subordination of taxa were established in accordance with the time of their historical origin, being manifested by a hybridization distance indicator of $\Delta T_{50}H$, where T_{50} is the temperature in degrees of Celsius in an ideal normalized cumulative frequency of distribution, at which 50% of all potentially hybrid single-copy DNA-sequences are in a hybrid form, while 50% are separated. At that, $\Delta T_{50}H = 1.0$ corresponded to 4.5 million years of evolution, which was calibrated on the basis of the evolution of passerine birds, where the indicator of the order $\Delta T_{50}H = 20-22$. For constructing dendrograms, Sibley and Ahlquist used the special programs FITCH and KITSCH, the first of which displayed both a branching pattern and a scale of differences between taxa reflected in the length of the branches. This monograph provided the basis and reference point for numerous subsequent analyses of the evolution of birds, not the least of which were of passerine birds, both in terms of the historical aspects of their formation and their subsequent diversification (Barraclough et al., 1995; Cardillo, 1999; Ericson et al., 2000, 2002, 2003; Cracraft, 2001; Irestedt et al., 2001; Ricklefs, 2003, 2006; Barker et al., 2004).

In the new classification, using the results of DNA hybridization, Sibley and Ahlquist (1990) created a superorder of Passerimorphae, which includes, besides Passeriformes, the orders of Columbiformes, Gruiformes, and Ciconiiformes, and all Passeriformes were departed from this clade of non-passerines. Also, a parvclass Passerae was formed, which included, besides the superorder asserimorphae, the orders of owls (Strigiformes), turacos (Musophagiformes), hummingbirds (Trochiliformes), swifts (Apodiformes), parrots (Psittaciformes), and cuckoos (Cuculiformes) (Fig. 1).

The data on the phylogeny of passerines allowed Sibley and Ahlquist (1990) to confirm the traditional division of passerines into two suborders—Tyranni for suboscine passerines and Passeri for oscine passerines. These two groups were clearly different in terms of the measures of DNA−DNA distances, in addition to the morphological differences,. However, Sibley and Ahlquist hypothesized that many oscines of the Australia−New Guinea region form a monophyletic group—the parvorder Corvida, which is a sister group to all the remaining oscines forming a monophyletic group, the parvorder Passerida (Fig. 2). This hypothesis suggested an autochthonous adaptive radiation of the oscines within Australia, as well as the fact that some lineages of birds of the New and Old World, such as crows (*Corvus*), jays (*Garrulus, Gymnorhinus*), and cuckooshrikes (Campephagidae), have their roots in Australia rather than in the tropics of the Old and New World, where they currently have achieved great diversity. These views were supported by new data from fossil finds and the reconstruction of paleobiotopes, which pointed to a tropical rainforest in Australia at
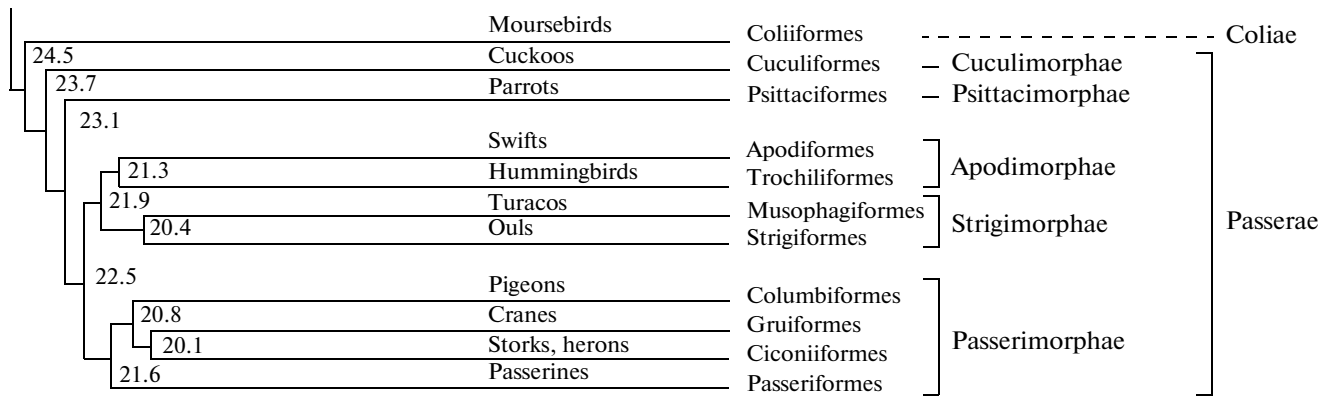
Fig. 1. Composition of parvclass Passerae according to DNA hybridization data (from Sibley and Ahlquist, 1990).
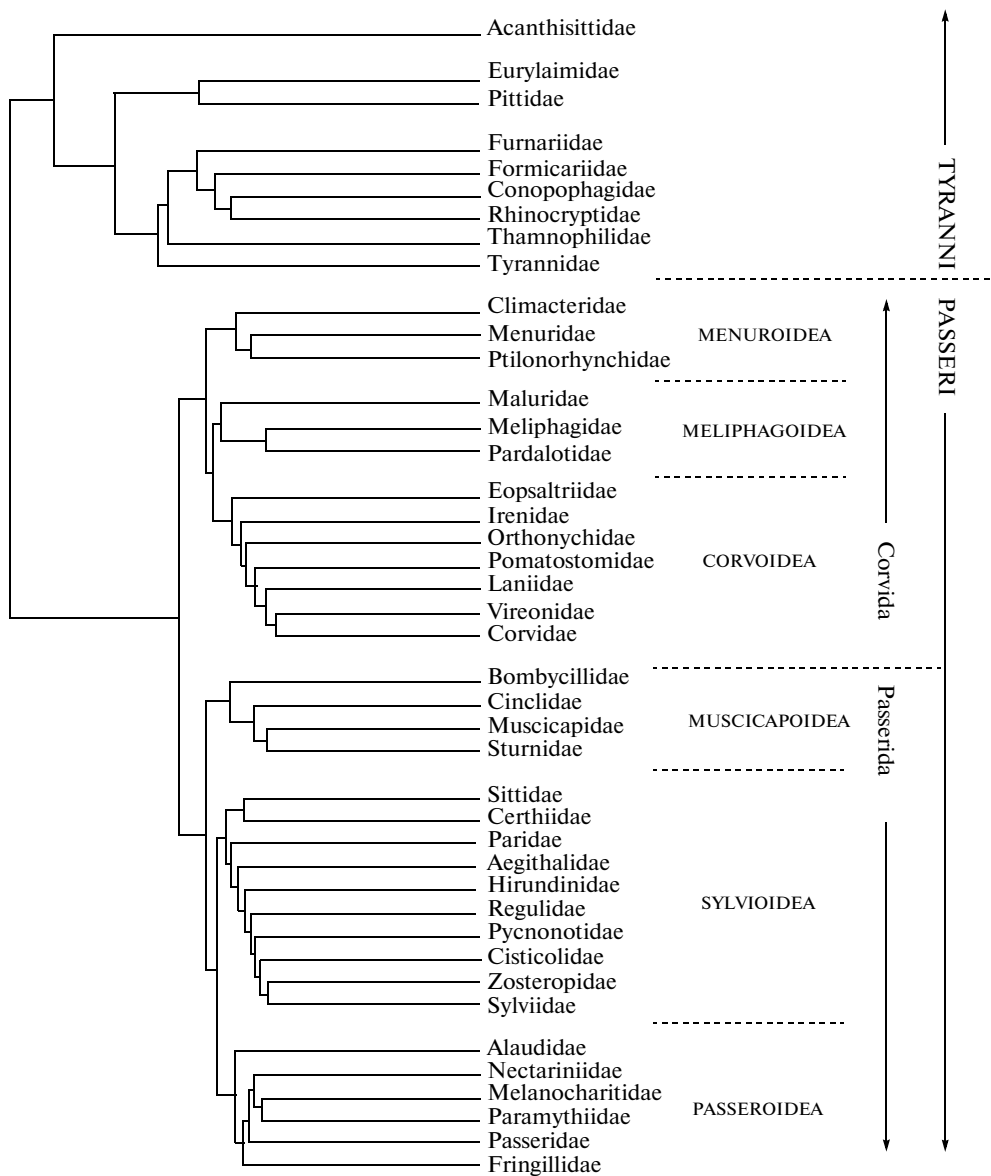

Fig. 2. Phylogenetic relationships of passerine families according to DNA hybridization data (Sibley and Ahlquist, 1990).

that time as a place of rapid adaptive radiation (Edwards and Boles, 2002).

Corvida included, first, the superfamily Corvoidea, consisting of the family Corvidae, which also included birds from the traditional families of birds-of-paradise, old world orioles (Oriolidae), drongo (Dicruridae), paradise flycatchers (*Terpsiphone*), woodswallows (Artamidae), and fantails (Rhipiduridae). Besides Corvidae, the superfamily Corvoidea included families of vireos (Vireonidae), shrikes (Laniidae), Australo-Papuan babblers (Pomatostomatidae), logrunners (Orthonychidae), leafbirds (Irenidae), and Australasian robins (Eopsaltriidae). Second, Corvida included the superfamily Meliphagoidea, consisting of the families of honeyeaters, wren-warblers (Maluridae), and diamondbirds (Pardalotidae), as well the superfamily Menuroidea, consisting of the families of lyrebirds, Australasian treecreepers (Climacteridae), and bowerbirds (Ptilonorhynchidae).

Thus, the parvorder Corvida included birds that were common in Australia and the New Guinea area, and several of these families included species converged to species from the families of another parvorder, Passerida, from the Old and New World.

The parvorder Passerida, by Sibley and Ahlquist (1990), includes three very large superfamilies—Passeroidea, Sylvioidea, and Muscicapoidea (Fig. 2). The superfamily Passeroidea consists of the families of passerines (Passeridae), true finches, painted berrypeckers (Paramythiidae), berrypeckers (Melanocharitidae), sunbirds, and larks. Here we must emphasize that into the family of passerines, besides the subfamily of sparrows (Passerinae), Sibley and Ahlquist placed weavers (Ploceinae) and estrildid finches (Estrildinae), as well as the subfamilies of wagtails and pipits (Motacillinae) and accentors (Prunellinae). The superfamily Sylvioidea, to the surprise of ornithologists, consists, according to Sibley and Ahlquist, not only of the families of Old World warblers, white-eyes (Zosteropidae), cisticolas (Cisticolidae), and goldcrests (Regulidae), but also of bulbuls (Pycnonotidae), swallows, longtail tits (Aegithalidae), tits, treecreepers (Certhiidae), and nuthatches (Sittidae), and the treecreepers also include wrens and gnatcatchers (*Polioptila*). And in the superfamily Muscicapoidea, in addition to the family of Old World flycatchers, Sibley and Ahlquist also included dippers, starlings (Sturnidae), and waxwings (Bombycillidae).

Thus, in the new classification based on the data of DNA hybridization (Sibley and Ahlquist, 1990), passerines underwent a very large revision, both at the level of families and at higher levels. By their monograph, these authors have provided more information for ornithologists to discuss and debate than any other bird taxonomists of the 20th century. DNA hybridization studies, along with morphological analyses of the same time (Raikow, 1987; Prum, 1993), independently gave quite a similar pattern of branching of the main divisions of the tree of passerines, where this pattern was significantly different from the previous ones. The opinion on the "primitiveness" of lyrebirds, as well as broadbills and scrub-birds (Atrichornithidae), has changed. It was recognized that suboscines consists of two monophyletic groups, those of the Old and New Worlds. Suboscines of the Old World, the families of pittas (Pittidae) and broadbills, are concentrated in Africa and South-East Asia and are poor in their species composition, despite the high degree of morphological differences. In contrast, the adaptive radiation of suboscines of the New World is very extensive (about 1100 species, mostly endemic to South America), and they are extremely diverse in morphology and behavior, being composed of the families of tyrant flycatchers (Tyrannidae), -antshrikes (Thamnophilidae), tapaculos (Rhinocryptidae), gnateaters (Conopophagidae), ground antbirds (Formicariidae), and ovenbirds (Furnariidae).

As a result of all the studies of passerines in the late 20th century, the understanding of the phylogeny of the order has greatly improved. The morphological cladistic analysis and DNA hybridization studies have generally given a quite similar pattern of branching of the main divisions of the tree of passerines. The linear classifications of previous taxonomists have been replaced by hierarchical classifications based on the concept of phylogeny (Raikow, 1987; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; Raikow and Bledsoe, 2000).

PHYLOGENY AND EVOLUTION OF PASSERINES ACCORDING TO DNA SEQUENCING DATA

Despite the great success of the studies set forth by Sibley and Ahlquist (1990), it soon began to be criticized with respect to various aspects of the phylogeny proposed (Cracraft, 1992; Edwards and Boles, 2002; Ericson and Johansson, 2003; Barker et al., 2004). However, the phylogeny and classification by Sibley and Ahlquist of passerine birds with 42 families became the basis for subsequent analyzes. In 2002—2005, articles on the results of studies on nuclear DNA sequencing of passerines were published (Barker et al., 2002; Ericson et al., 2002, 2003; Ericson and Johansson, 2003; Chesser, 2004; Beresford et al., 2005). These works clearly confirmed the division of all Passeriformes into two monophyletic clades—suboscines and oscines. Second, and most importantly, it was found that a family of small, so-called New Zealand "wrens," Acanthisittidae (or Xenicidae), having only four species, is nothing more than a sister group of all other passerines. This family of birds has long been a taxonomic riddle and ornithologists have been interested in their obscure state and specific morphological traits. In these birds, the syrinx has no specific features inherent to the syrinx of oscines, and at the same time, the bone of the middle ear has no bulbar shape, which is typical for all suboscines (Feduccia, 1975). Sibley
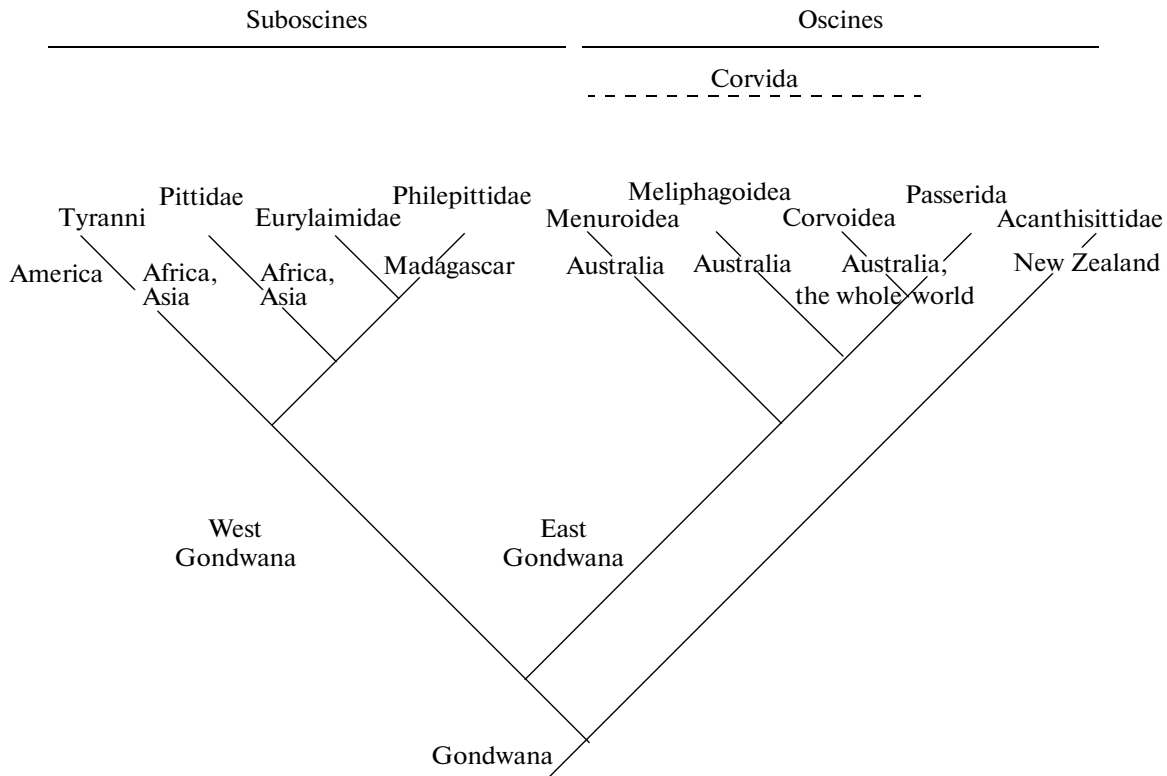
Fig. 3. Cladogramm of major groups of passerines according to nuclear DNA sequencing, their present distribution and suggested origin from Gondwana (Ericson et al., 2002).

and Ahlquist (1990) placed them among the base of suboscines, assuming this by the molecular clock, and Raikow (1987) identified them as a sister group of the oscines, relying on the morphology of one of the leg muscles that appear in oscines as atavistic anomaly.

Later, in the next paper of Barker et al. (2004), based on the sequencing of the two single-copy nuclear genes from 144 passerine species from 45 families, phylogenetic analysis confirmed the findings of previous studies on DNA sequencing (Barker et al., 2002; Ericson et al., 2002) and found significant discrepancies with the branching of the tree of passerines according to the data of DNA hybridization (Sibley and Ahlquist, 1990). This led Barker et al. (2004) to assume that the phylogeny by Sibley and Ahlquist, as well as the taxonomy that was partly based on it (Sibley and Monroe, 1990), is highly problematic. All new studies recognized the impossibility of supporting the hypothesis of Sibley and Ahlquist (1990) on the parallel diversification of the northern, Afro-Eurasian Passerida, and southern, Australian-New Guinean Corvida, and their relationship as sister groups. According to the new data (Barker et al., 2004), Passerida is part of a paraphyletic group Corvida, indicating that songbirds had originated not in the north, in Eurasia, but in Australia and New Guinea as part of East Gondwana (Fig. 3).

Up to 1970s−1980s, ornithologists believed that various Australian and New Guinean "wrens,"

"treecreepers," and "robins" are recent derivatives of the corresponding groups in Eurasia and America. The first doubts began to come in from paleontologists. The assumption about the origin of passerines in the Southern Hemisphere has long been suggested (Feduccia and Olson, 1982). Prior to the Middle Miocene, a very small number of songbirds were found, and the earliest finds were dated to the Upper Oligocene of France. From this it followed that songbirds originated in the Southern Hemisphere, and then spread to the north (Olson, 1988). However, there was not enough evidence to test this hypothesis, until two small bones in the Early Eocene sediments in the south-east Queensland, Australia were found (Boles, 1995). These findings pushed back the age of passerine birds by almost 25 million years, to the time when Australia had already begun to separate from eastern Antarctica.

The phylogenetic relationships within Passerida, according to the new data (Ericson and Johansson, 2003; Ericson et al., 2003; Barker et al., 2004; Beresford et al., 2005), also demanded a revision. There were doubts in the position of waxwings at the base of Muscicapoidea, as well as in the whole group of Sylvioidea, in particular, the phylogenetic relationships of kinglets and the clades composed of treecreepers, wrens, and nuthatches. Monophyly of the Old World warbler family also was not supported.
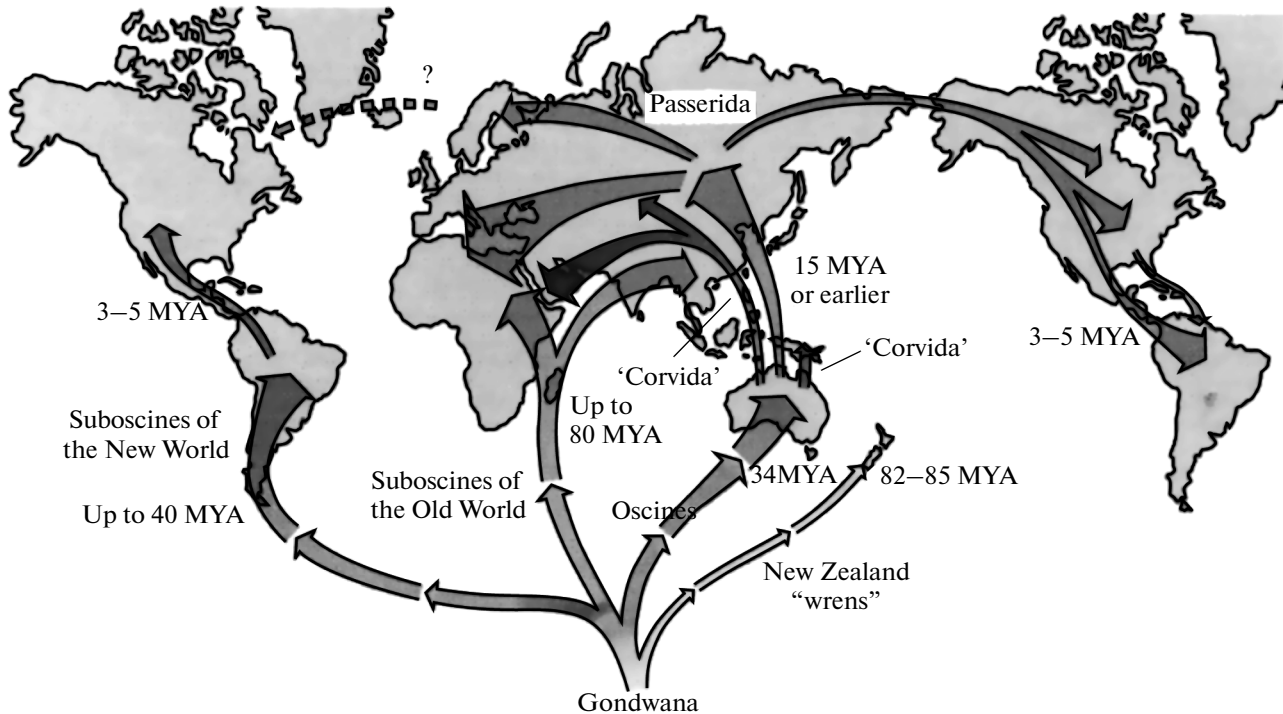
Fig. 4. Suggested dispersal routes of major passerine groups from Gondwana based on the data of phylogenetic relationships and biogeography (Ericson et al., 2002). MYA stands for "millions years ago."

In the study of the phylogeny of the songbirds using nuclear DNA sequencing (Treplin et al., 2008) based on a new molecular marker ZENK, along with three conventional RAG-1, RAG-2, and c-*myc*, some new data were obtained. This analysis was carried out with the clear support of the dividing the group Passerida (in the sense of Sibley and Ahlquist, 1990) into three superfamilies, of which Sylvioidea is a sister taxon for Muscicapoidea and Passeroidea. It was confirmed that Sylvioidea are not monophyletic. It was strongly supported that the family of tits should be separated from all other Sylvioidea, just as was previously expected (Alström et al., 2006). The position of larks remained unclear; there is evidence that they form a sister taxon to all other Sylvioidea, but according to another analysis they form a monophyletic group with swallows. The position of a number of genera and species in the family Acrocephalidae (*sensu* Alström et al., 2006) is equally contradictory. The Common Grasshopper Warbler (*Locustella naevia*) forms a monophyletic group with genera *Acrocephalus* and *Hippolais*, but according to other sources, it is a basal sister taxon of Sylvioidea. Also it is still at issue whether *Acrocephalus* and *Hippolais* are monophyletic (Helbig and Seibold, 1999).

The monophyly of suboscines of both the Old and the New World suggests that these groups of birds were divided a long time ago, and there are two versions of the circumstances of such a separation. One is based on the hypothesis that suboscines were widespread before the separation of Africa and South America, and that they divided when the continents separated.

But this is not consistent with the separation time of the continents, that is, earlier than 90 million years ago. Another version (Ericson et al., 2003) seems more probable; the Kerguelen Plateau (now underwater in the Indian Ocean) separated from Antarctica in the Late Cretaceous, and suboscines of the Old World could spread to Africa and Asia over this plateau (Fig. 4).

Although most of the previous systematic works on suboscines were based on morphological traits, the work on DNA hybridization (Sibley and Ahlquist, 1990) presented a scheme of their phylogeny that coincided with traditional by several provisions. However, according to these data, the traditional families of tyrant flycatchers and ground antbirds were polyphyletic, which in regard to the latter family was supported by the DNA sequencing data (Irestedt et al., 2002). The detailed phylogenetic relationships among suboscines of the New World were studied (Chesser, 2004) on the basis of sequencing data of both the nuclear and mitochondrial DNA in a sample of 53 taxa, of which 44 are suboscines of the New World, three are suboscines of the Old World, four are oscines, and one species is the New Zealand Rifleman (*Acanthisitta chloris*), and one species of woodpecker (*Campethera nivosa*) as an outgroup. The results of the analysis confirmed that New Zealand wrens are indeed a sister group to all other passerines, which coincides with the findings of previous studies (Barker et al., 2002; Ericson et al., 2002). Second, suboscines and oscines make up two distinct monophyletic groups. As for suboscines of the New World, one of its representatives, the

Broad-billed manakin (*Sapayoa aenigma*), a resident of rainforests from Panama to Ecuador, suddenly appeared to be suboscines of the Old World. If one excludes this species from the analysis, the monophyly of the remaining suboscines of the New World is clearly supported by all the molecular data. The monophyly of the clades of ovenbirds and tyrant fly-catchers is confirmed among them, although the monophyly of tyrant flycatchers can be maintained only if the subfamily Tityrinae is excluded from this family. As for the family of ground antbirds, it really turned to be polyphyletic. The genus *Melanopareia* and the Sharpbill (*Oxyruncus cristatus*) remained of unclear relationship.

The tyrant flycatcher family, which is more than one third of all species of suboscines of the New World (about 400 species in 100 genera), was phylogeneti-cally studied based on sequencing DNA from three nuclear introns of 128 taxa (Ohlson et al., 2008). The results confirmed a lot in the field of kinship relations in the family. In particular, a group of tityres indeed makes up a separate family Tytyridae, and some genera of tyrant flycatchers, such as the Royal Flycatcher (*Onychorhynchus*), the Ruddy-tailed Flycatcher (*Tere-notriccus*), and myiobius (*Myiobius*), which are usually referred to tyrant flycatchers, should be derived from this family and perhaps may be related to tityres. The very family Tyrannidae consists of two main lineages. One of them is the clade of the subfamily Pipromor-phinae (flat-billed tyrant flycatchers, todies, antpipits, *Phylloscartes*, and spectacled bristle tyrants). The sec-ond clade is divided into two subclades, one consists of Elaeniinae (*Elaenia*, tit-tyrants, *Phyllomyias*, etc.), and the second of the three groups—Myiarchinae (genus *Myiarchus*, etc.), Tyranninae (tyrant pirate, etc.), and Fluvicolinae (genus *Myiophobus*, etc.). Attempting to reconstruct the habitats of the ancestors of these birds and an estimation of the time of diver-gence suggests that the basic events of divergence of Tyrannidae took place in the wet forest during the Oli-gocene. Large-scale diversification in open habitats was inherent to birds from the groups Elaeniinae, Myiarchi-nae, Tyranninae, and Fluvicolinae since the mid-Miocene, that is, about 15 million years ago.

One of the genera of tyrant flycatchers, black tyrants (*Knipolegus*), was provided with the first molecular phylogenetic hypothesis based on the sequencing of the nuclear and mitochondrial DNA (Hosner and Moyle, 2012). The analysis determined monophyly of the genus, with its most likely sister group of the genus *Lessonia*. The genus *Knipolegus* forms three clades: the first is of three species limited in spread by the northern part of South America; the second is again of three species found in southeastern Brazil; and the third clade is formed of six species widespread in the southern part of South America.

Of the further works on bird DNA sequencing, two are the most remarkable. The first is the publication by Hackett with 17 co-authors (Hackett et al., 2008), based on a study of 32000 heterocyclic bases of aligned sequences of the nuclear DNA from 19 independent genes in 169 species representing all the major groups of birds. This work gave a completely new picture of phylogenetic relationships. This system significantly differs from previous classifications based on research of the morphology and DNA hybridization and previ-ous studies of DNA sequencing, both nuclear and mitochondrial. Non-monophyly of a series of a tradi-tionally taken number of orders of birds was shown. For example, Apodiformes appeared as part of the radiation of nightjars, woodpeckers became part of Coraciiformes, and grebes (Podicipediformes) turned out to be closely-related to flamingos (Phoenicopteri-formes). Diurnal birds of prey (Falconiformes), tradi-tionally consisting of falcons (Falconidae) and Accip-itrides? (Accipitridae), were included in different branches of the tree of birds. The previously alleged relationships between the New World vultures (Cathartidae) and Ciconiiformes were not confirmed.

As for passerine birds, Hackett et al. (2008) confirmed the inviolability of dividing them into oscines and subos-cines, as well as a special base position of the New Zealand wrens with respect to all Passeriformes. It was shown that passerines are included in the biggest clade— the clade of ground birds, also consisting of woodpeckers, diurnal raptors, owls, rollers, parrots, mousebirds, and trogons. Most unexpected in this case are the relation-ships of sister groups between passerines and parrots and a sister relation of this clade to the clade of falcons. At the same time, accipitrides are quite distanced from them, being close to the owls (Fig. 5).

Another recent significant publication (Pacheco et al., 2011) reports on a new analysis of the time of origin and evolutionary relationships among the orders of modern birds based on the use of complete mitochondrial genomes, which, as the authors say, are the main sources of data for studies of the evolution of birds. This paper, based on 80 complete genomes, of which 17 are new in such studies, analyzes many taxa of modern birds from the Old and New Worlds. Although the discussed paper showed moderate con-sistency of the results of molecular studies with a num-ber of traditional views (Payevsky, 2012), many of these results occurred to be as new as the data of Hack-ett et al. (2008). It has shown a common origin of nightjars, swifts, and cuckoos, as well as the face that Columbiformes and Charadriiformes are monophyl-etic and are sister groups. Passerines in this work, as in all the previous studies, are recognized as a monophyl-etic group together with suboscines and oscines as two separate clades, together with New Zealand wrens as a sister group. However, the suggested relation of passe-rines and parrots as sister groups and falcons as a closely related group (Hackett et al., 2008) was not confirmed by this analysis. Instead, a clade with branching into parrots and owls was found, which had a common ancestor with passerines, rollers, wood-peckers, and trogons (Fig. 6).
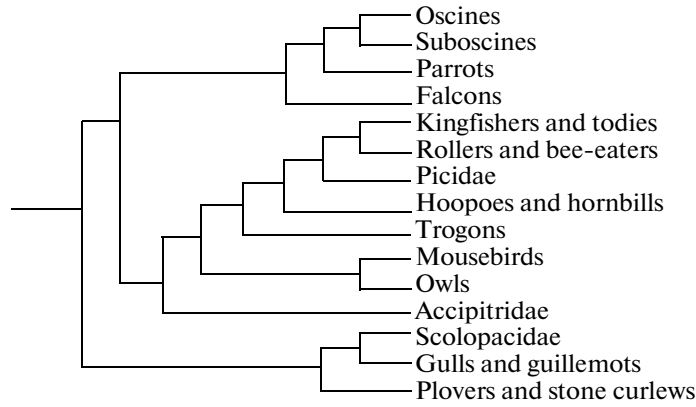
Fig. 5. Part of phylogenetic tree of birds according to nuclear sequencing data. Simplified scheme of cladogram (Hackett et al., 2008).
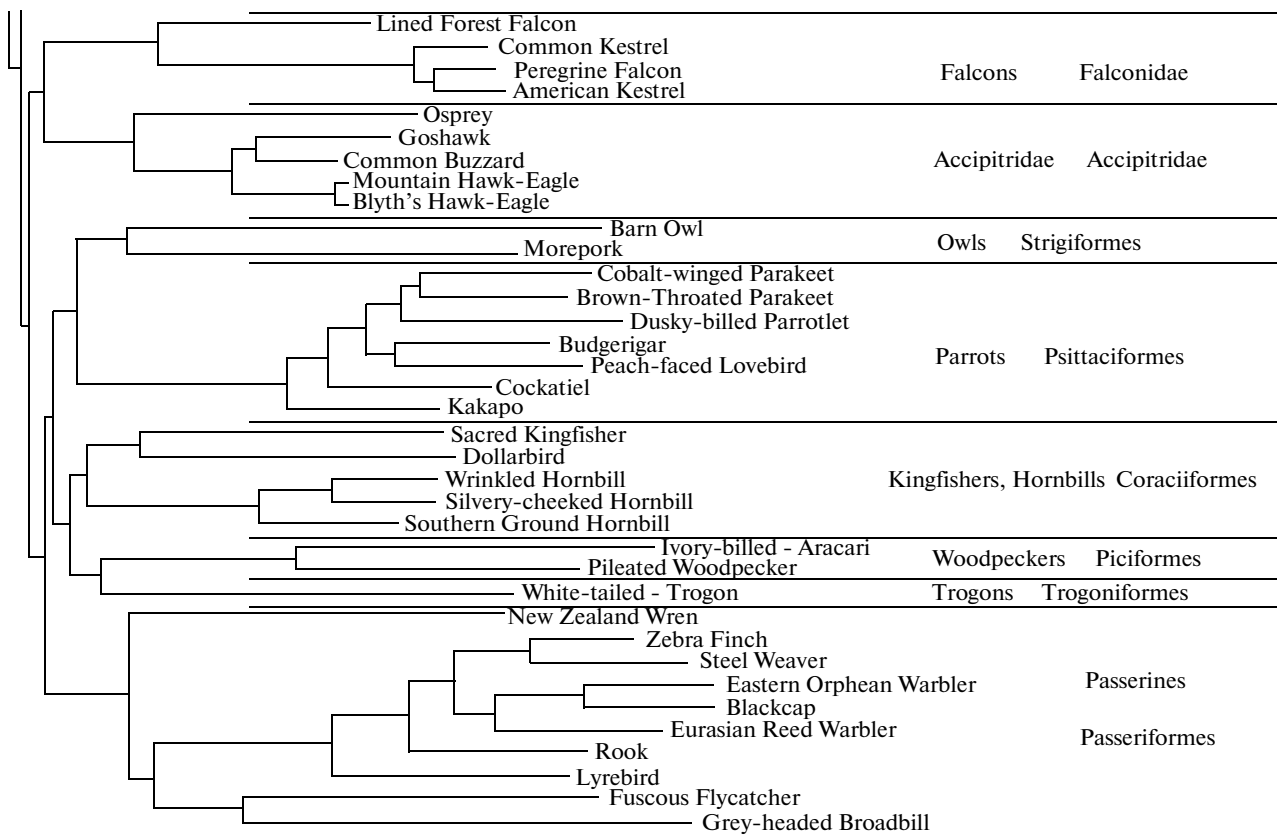

Fig. 6. Phylogenetic relationships among seven orders of birds according to data of sequencing complete mitochondrial genomes (Pacheco et al., 2011).

PHYLOGENY OF CHAT-FLYCATCHER COMPLEX (MUSCICAPIDAE sensu DICKINSON, 2003)

From molecular studies on phylogeny of individual groups of passerines at the family level, two works on studying the complex chats–flycatchers (when the group of chats also includes wheatears), based on a combination of nuclear and mitochondrial sequenc-ing, may be of interest (Zuccon and Ericson, 2010; Sangster et al., 2010). Until recently, according to the traditional view of taxonomists (for example, Wet-more, 1960; Kartashev, 1974), chats with wheatears were attributed to thrushes, and Old World flycatchers were isolated into the family Muscicapidae. It has long been known that chats, wheatears, and flycatchers have morphological and behavioral similarities. The

genus *Muscicapa* (subfamily Muscicapinae) was usually considered close to thrushes. According to the taxonomy of Mayr and Amadon (1951), the volume of the Old World flycatcher family was the largest since at the rank of subfamilies. Besides flycatchers, it included thrushes, babblers, Old World warblers, kinglets, wrens, dippers, and mockingbirds. In the list of birds of the world (Dickinson, 2003), the family Muscicapidae includes chats, wheatears, flycatchers, robins (*Erithacus*), nightingales (*Luscinia*), redstarts (*Phoenicurus*) and many other taxa (in total, 275 species in 48 genera). Species of this family are widely distributed in different regions of the world, living in a variety of habitats.

The proximity of thrushes and Old World flycatchers was mostly based on two synapomorphies—features of the syrinx morphology and mottled plumage of young birds. Some studies of the subfamilies Turdinae and Muscicapinae considered them as sister groups (Sibley and Ahlquist, 1990; Barker et al., 2004; Johansson et al., 2008), although other studies (Zuccon et al., 2006; Voelker and Spellman, 2004) did not suggest close relationships between them, and at the same time the views that Old World flycatchers and chats make up one monophyletic branch were confirmed. According to some molecular studies (Cibois and Cracraft, 2004; Voelker and Spellman, 2004), a typical Old World flycatcher of the genus *Ficedula* and the rock thrush *Monticola* belong to the subfamily of stonechats Saxicolinae, while shamas *Copsychus*—to Old World flycatchers.

To analyze the phylogenetic relationships using the data of nuclear and mitochondrial sequencing in the chat-flycatcher complex (Zuccon and Ericson, 2010), 46 species were selected from Saxicolinae and 20 species from flycatchers, as well as six species of thrushes as an outgroup, representing the main lines of Turdidae; the analysis was carried out using Bayesian probability and maximum likelihood criterion. The results showed that the commonly accepted separation of ground feeding stonechats and wheatears and air-feeding flycatchers does not reflect the existence of monophyletic groups. Morphological adaptations for air feeding (broad beak, perioral bristles, short tarsometatarsus) and the typical behavior of flycatchers apparently evolved independently in the three lineages. Always believed to be thrushes, the genera of whistling thrushes (*Myiophonus*), shortwings (*Brachypteryx*), and alethes (*Alethe*) turned out to belong to the family of Old World flycatchers, and their morphological and ecological similarity with true thrushes, apparently, is the result of convergence. One of the main lineages includes three clades—*Alethe*, the clade of African flycatchers (*Sigelus, Myioparus, Melaenornis, Fraseria, Empidornis*, and *Bradornis*) and birds of the genus *Muscicapa*, and finally the clade of the genera *Erythropygia, Cercotrichas, Copsychus, Saxicoloides*, and *Trichixos*.

The genus *Erithacus* turned out to be a part of the group of African "robin-like" birds (*Stiphrornis, Cossypha, Pseudalethe, Cichladusa, Pogonocichla,* and *Sheppardia*), and the genera *Luscinia, Tarsiger*, and *Enicurus* belong to the large Asian clade. The clade of redstarts (*Phoenicurus, Chaimarornis*, and *Rhyacornis*) is in the base of a group of genera together with *Monticola, Saxicola, Oenanthe, Cercomela*, and others (Zuccon and Ericson, 2010). According to the data of another analysis (Sangster et al., 2010), the position of the European robin (*Erithacus rubecula*) in the clade of African species and sisterly relations among *Ficedula* and *Monticola, Phoenicurus, Saxicola*, and *Oenanthe* were clearly confirmed.

PROBLEM OF PHYLOGENY OF "NEW WORLD NINE-PRIMARIED OSCINES"

Since the 19th century, the number of primary feathers of passerine birds has been seen as a taxonomic trait, and one group of birds was called "passerines with nine primaries," in contrast to passerines with ten primaries of varying degrees of development. Links have been found between the number of primaries and other traits; for example, it was believed that in passerines with ten well-developed primaries the vocal apparatus is of imperfect development (Wallace, 1874). The group of birds with nine primaries initially included the families Hirundinidae, Motacillidae, Bombycillidae, Dicaeidae, Mniotiltidae (now Parulidae), Coerebidae, Drepanididae, Tanagridae (now Thraupidae), Icteridae, and Fringillidae. Of these families, at present, the group of the "New World nine-primaried oscines," also called the "Fringillidae clade" (Sibley and Ahlquist, 1990), include Parulidae, Coerebidae, Drepanididae, Thraupidae, Icteridae, Fringillidae, and the American sparrows from Emberizidae, and had sometimes included Vireonidae, since the latter may have both nine and ten primaries. At the same time, despite the widespread use of this term to this day, many authors point out that in fact all of these birds have 10 primaries, but that the 10th one (or first, if one counts the primaries not centrifugally but centripetally) is reduced, sometimes to a very large extent. The most comprehensive and detailed study of the problem of one rudimentary feather out of ten primaries was carried out by Stegmann (1962), who showed there are actually always ten primaries, but one of them can be of very different lengths. The same conclusion was reached by Hall (2005) on the basis of a special study of 104 species of birds. She proved that, while being extremely rudimentary, the 10th primary (or first, by centripetal counting) is hidden under the covert feather of the previous (or subsequent) flight feather; only when lifting the latter one can see it.

Sibley and Ahlquist (1990) assumed the monophyly of the so-called New World nine-primaried oscines according to the data of DNA hybridization. The DNA sequencing analysis generally supports this

monophyly if they are not added with the family of true finches (Ericson et al., 2003), but in terms of the relationships within the group there is no agreement. The most clearly supported opinion based on both nuclear and mitochondrial genes states that Icteridae and Parulidae are sister groups. Surprisingly, according to the molecular data, the genera *Calcarius* (Lapland Longspur) and *Plectrophenax* (Snow Bunting) are not included in the group of American buntings and are in a basal position to all other "nine-primaried oscines." Most likely, the ancestors of the latter arrived in North America either from Asia via the Bering Strait or from Europe via Greenland, and the Lapland Longspur and Snow Bunting are descendants of earlier immigrants from the Old World (Ericson et al., 2003).

DEMOGRAPHIC PARAMETERS AND SPECIATION RATE

An important issue in the construction of relationships consists in the relation of demographic factors and the DNA evolution rate. The assumption that the generation lifetime duration affects the rate of accumulation of mutations in the DNA, and hence the rate of the genome evolution (Kohne et al., 1972), led to the logical conclusion that the shorter the generation lifetime was, the higher the rate of molecular evolution would be. Initially, a single-copy DNA comparison in long-lived and short-lived birds (in the example of Procellariiformes) did not confirm this finding (Sibley and Ahlquist, 1983), but later it was found to be erroneous (Sibley and Ahlquist, 1990). In birds with delayed sexual maturity and a long generation lifetime, the DNA evolution rate is slower than in birds that begin to breed at an early age and have a short generation lifetime. The latter include the vast majority of passerines (as well as Columbidae, Galliformes, some waterfowl) that begin to breed at the age of one year (Ricklefs, 1972; Payevsky, 1985). Therefore, the increased rate of their evolution can be explained by peculiarities of their demographics. Anyway, these species had similar rates of changes in the genome, which has been shown by branches that are longer or of the same in length in the dendrograms when compared to the groups with very different lifetimes of generations. In some cases, when a species starts to breed at the age of less than one year, such as estrildid finches, the branches are longer than those branches of their closely related forms with reproduction at a later age (Sibley and Ahlquist, 1990).

The optimum values of species diversity are dependent on the degree of stability of the environment, where this degree is expressed in the intensity of resource flows; when they increase, these values increase as well. Thus, resources are used more efficiently because of the differentiation of ecological niches (Bukvareva and Aleshchenko, 2010). The extensive material and discussion of differences in this respect among the clades of passerines of different sizes and different regional habitats are presented in two papers by Ricklefs (2003, 2006) on global variation in the diversification rate of passerines. The existence of significant variations in the level of species diversity of different clades of birds led to the idea that activation of the diversification rate occurs at certain key innovations, such as promiscuity, plumage dichromatism, and other phenomena due to sexual selection. However, the search for key innovations is very difficult because of the different ecology, lifestyle, and geographic distribution. The hypothesis of the existence of a higher diversification rate in the tropical latitudes due to high air temperatures and intense energy flow has been repeatedly discussed (Allen et al., 2002; Ricklefs, 2006, etc.). This hypothesis was tested by comparing sister taxa, as they are of the same age. However, the difficulty of selecting sister clades that have primary differences in the latitudinal distribution did not permit latitudinal comparisons in the raw, without the influence of other factors. To solve this problem, Ricklefs (2006) compared the rate of diversification among clades in several taxa of passerine birds that were endemic to the tropics and the temperate zone of America. As a result, it was found that the net rate of diversification of passerine birds is significantly higher in both the larger areas and the tropical regions. At the same time, the rates of diversification decrease with the age of clades, and this suggests that the filling of the ecological space limits further diversification.

In connection with the above data, the question arises of the existence of differences in the level of divergence between species. The assessment of the degree of genetic differentiation between populations and species in terms of the share of structural genes in the compared taxa is implemented in the index of genetic distance. The comparison of genetic distances between species showed that in birds they are minimal in relation to the genetic distances in other species of animals: three times less than in mammals, five times less than that of reptiles, and more than ten times less than that of amphibia (Borkin and Litvinchuk, 2010). It is still unknown whether these differences are associated with the speciation rate.

CONCLUSION

This review shows that the extraordinarily rapid development of contemporary molecular research aimed at the study of the systematics of birds leads to results that from the standpoint of traditional views often seem strange, unexpected, and sometimes erroneous (Cracraft, 1992; Balatskii, 1997; Koblik, 2001). As E.A. Koblik rightly pointed out (2001), it comes to the absurd situation where representatives of genera that are known to be close in terms of a complex of traits are assigned to different families. The paradox of the situation is aggravated by the fact that each new molecular study of phylogenetic relationships of birds of both higher taxa and others largely rejects findings

of previous authors and promotes new perspectives on the basis of their results. Numerous examples of systematic innovations in the order of passerine birds, discussed above, clearly demonstrate this.

Can one expect real progress, accepted by a majority of taxonomists, in this area? Presumably, only an integrated approach, with the use of different molecular studies and conventional comparative morphological analysis, may lead to such progress. With varying degrees of certainty, this is demonstrated by those provisions that exist today in the phylogeny of higher taxa of passerine birds. Some of them are "unshakable," supported by both morphological and different molecular data: (1) the division into two suborders, Oscines and Suboscines; (2) the special systematic position of New Zealand wrens; and (3) the division of Suboscines into groups of birds of the New and Old Worlds. Other provisions are probable, supported by some morphological and some molecular data, for example, the close relationships among the groups of woodpeckers, rollers, and trogons. And, finally, there are the controversial provisions, supported only by some molecular data: (1) the diversion of the clade of passerines from the clade containing cranes and storks, (2) the relations of sister groups between passerines and parrots, and (3) the proximity of passerines to falcons.

In conclusion, we can express cautious optimism that the current research of avian taxonomy will include a comparison of molecular, morphological and behavioral traits along with the broad involvement of biogeographical and ecological discussions in order to ascertain the true phylogeny and evolutionary paths.

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