# The Concept of Bird Species: Theory and Practice

E. A. Koblik<sup>a, \*</sup>, Ya. A. Red'kin<sup>a</sup>, S. V. Volkov<sup>a, b</sup>, and A. A. Mosalov<sup>c</sup>

<sup>a</sup>Zoological Museum, Moscow State University, Moscow, 125009 Russia <sup>b</sup>Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia <sup>c</sup>Institute of Biology and Chemistry, Moscow State Pedagogical University, Moscow, 129164 Russia \*e-mail: koblik@zmmu.msu.ru

Received February 7, 2019; revised February 12, 2019; accepted February 15, 2019

Abstract—As it has presently become evident, reproductive isolation can no longer be considered as the leading criterion for estimating the species limits, but it is still used for determining the status of the majority of morphs. The presence/absence of hybridization between individuals is not directly related to the degree of their evolutionary insularity. Hybridization can result in the origin of new morphs including those that have species status. The application of phylogenetic methods is justified in reconstructing the relation links within complex groups including the morphs of various evolutionary levels (from geographical races to "good" species), the relationships between which are exacerbated by hybridogenous polymorphism and/or the hybridization origins of their populations. Taking into account both new data and new conceptions, we suggest genuine interrelated definitions of concepts such as species, subspecies, and semispecies in birds. The definitions are based on two main criteria: biological, i.e., an evaluation of the reproductive relations of the particular morphs with each other, and phylogenetic, i.e., an evaluation of their evolutionary age and kinship. The main feature of a species as an evolutionary entity should be considered through its stability in time even when its reproductive isolation is periodically broken. Geographic intraspecies races show sustainable variations of different degrees, but they have no reproductive isolation; they breed upon contact and form intergradation zones. They are taxonomically denoted as subspecies. Descriptions of new subspecies are viable to the limits that reflect the species' natural geographic structure to the fullest extent. For the young morphs that have reached the level of species insularity in the course of evolution, it seems appropriate to restore a semispecies category. Semispecies show significant morphological differences and distinguished ecological particularities, as a rule, but they are connected to closely related morphs by gene flows in contact zones. Distinguishing this category is not regulated by the International Code of Zoological Nomenclature and, as splitter tendencies prevail in modern systematics, semispecies are more often equated to species; i.e., they have binominal names. We propose to denote the attribution of a semispecies to a particular species group (superspecies) in parentheses between genus and species names. Thus, it would become possible to outline natural complexes and avoid a groundless increase in the taxonomic statuses of morphs in the stage of development. Representatives of distant phylogenetic lines (morphs that separated historically long ago) are not to be considered as semispecies even in the cases of their reproductive isolation being broken and a steady hybridization existing between them.

*Keywords:* taxonomy, species, semispecies, subspecies, geographic race, biological species concept, phylogenetic species concept, reproductive isolation **DOI:** 10.1134/S1062359020070079

**JOI:** 10.1134/**S**1062359020070079

# INTRODUCTION

The concept of species is one of the key concepts in biology and the basis of the biological systematics of living organisms. The number of recognized bird species in world reports periodically changes. After the adoption of the concept of a polytypic species, this number decreased from 18939 species in 1890–1909 to 8616 species in 1946 (Haffer, 1992, 1997), but has since grown again, now reaching almost 11000 species (Dickinson and Remsen, 2013; Dickinson and Christidis, 2014; del Hoyo and Collar, 2014, 2016). In the volume of *Illustrated Checklist of the Birds of the World* dedicated to the order Passeriformes (del Hoyo and Collar, 2016), only 41 cases of their association are counted in 628 cases of fragmentation of species. Similar "fragmenting" tendencies (concerning high taxa), accompanied by a complication of the ranking structure, prevail in the taxonomy of almost all the kingdoms of wildlife (Zhang, 2013; Averyanov and Lopatin, 2014). Indeed, during the revolution of the 1930s in taxonomy and the enlargement of "overly narrowly understood" species, many taxa lost their species rank undeservedly. With the accumulation and comprehension of data on the specifics of a number of morphs, such errors were gradually corrected (Stepanyan, 1983). At the same time, outwardly indistinguishable, usually allopatric morphs, previously considered conspecific, began to receive a species status. Genetic distances, facts of the absence of gene exchange, differences in vocalization, ecology, color details, etc., are cited as criteria for their selection. In a sense, we can speak of "taxonomic inflation" and "devaluation of the concept of species" (del Hoyo and Collar, 2014).

The recently developed polemic about "taxonomic discipline" and "taxonomic anarchy" (Garnett and Christidis, 2017; Thompson et al., 2018) has once again outlined an applied problem: depending on what kind of conception of species is used by taxonomists, representatives of one class of animals may be at greater risk than members of another class because they receive less funding for conservation. For example, in 2012, under the U.S. Endangered Species Act, approximately the same amount of funds was allocated to protect the genetic diversity of birds and more fractionally divided mammals. American ornithosystematics adhere to the biological concept of species (hereinafter BCS), which is considered by most taxonomists-theriologists as "conservative." With the adoption of the phylogenetic concept of species (hereinafter PCS), the number of bird species would double, and funding for their protection would increase accordingly (Garnett and Christidis, 2017). There is the opposing opinion that an increase in the number of recognized species does not depend on the transition to PCS (Sangster, 2009).

In the Russian-language ornithological literature, the increase in the number of species has been consistently criticized, speaking either from the position of a very narrowly understood BCS (Pfander, 2018) or from the position of the epigenetic theory of evolution (Mikhailov, 2003, 2015, 2017, 2018). Despite different worldviews, both authors support a return to a broad interpretation of the species, which generally corresponds to the concept of "zoogeographic species" (Haffer, 1997).

Thus, birds, having served as the main model in the process of emergence of BCS due to their specificity (primarily complex behavior), have become its "last bastion." At the same time, in recent years, a lot of research has been carried out that allows us to look differently at some of the criteria traditionally applied to the concept of "species" for representatives of the class Aves. Without pretending to philosophical generalizations, we found it useful to summarize new data and reformulate some concepts in the operational key.

## HYBRIDIZATION CRITERIA

The uncertainty of the criterion of reproductive isolation continues to be the weak point of the "classical" BCS (Panov, 1989). For this, BCS is rightly criticized by proponents of PCS. Obviously, understand-

ing the category of a species does not come down to its reproductive isolation (Panov, 1993). Numerous modern data indicate the widespread occurrence of regular interspecific hybridization in birds in nature (including those without any selective consequences): it has been observed between more than 850 species, i.e., one-twelfth of the composition of the world avifauna (Panov, 1989, 2001; McCarthy, 2006; Brelsford, 2011). In sympatric regions of related species, for example, the thrush (Luscinia luscinia) and common (L. megarhynchos) nightingales, up to 10% of pairs are mixed (Becker, 2007), and the proportion of morphologically distinguishable hybrids is even higher (Kováts et al., 2013). Hybridization between representatives of different genera and even families is also quite common (McCarthy, 2006).

In some cases, species rank morphs enter into hybridization, the scale of which is so significant that they lead to the emergence of a stable hybridogenic polymorphism and/or actual absorption of some populations of one species by another. Examples of such situations are the relations of representatives of the groups of "large white-headed gulls," "yellow wagtails," and "great gray shrikes" in relatively recent times (Panov, 1989, 1993; Liebers et al., 2004; Taykova and Red'kin, 2014; Red'kin et al., 2015, 2016).

A review by Lavrenchenko (2013) shows that, among mammals, only 15 species are of a supposedly hybridogenic origin, taking into account two polyploids and one intergeneric hybrid. Among birds, even fewer cases are known that could be confidently interpreted as the separation of hybrids into an independent species with the emergence of mechanisms that isolate them from both parental morphs. It is difficult to identify them using only molecular genetic or morphological methods, so justification requires an integrated approach, including an assessment of the morphological (at least) specificity and nature of reproductive relationships. The Italian sparrow (Passer italiae) began to be recognized as a hybrid species, and, according to formal characteristics, the goldencrowned manakin (Lepidothrix vilasboasi), whose range is delimited from the neighboring morphs by large rivers (Barrera-Guzman et al., 2017), and the Galapagos finch "Geospiza sp. nova," which formed in the course of just several generations (with achieving reproductive isolation), one of whose parents is the native species G. conirostris and the other is the recent invader G. fortis (Lamichhanev et al., 2017), can be considered as hybrid species.

The discrepancy of belonging to groups based on morphology, vocalization, and ecology with the results of phylogenetic constructions based on molecular data suggests that some species have a hybrid origin with unbalanced borrowing of parts of the genome and an equally uneven manifestation of the phenotype. In particular, such is the situation with the clus-



**Fig. 1.** Hypothesis of the hybridogenic origin of the Himalayan rubythroat (*Calliope pectoralis*), by Spiridonova et al., 2019 (as amended). Left: a diagram of two alleged interspecific hybridization events indicating the sex of birds of each parent species, which resulted in the emergence of the *C. pectoralis* subspecies: (I) the occurrence of *C. pectoralis*—ancestor of *C. p. confusa*, *C. p. pectoralis*, and *C. p. ballioni*; (II) the occurrence of the form *C. p. tschebaiewi*. Right: nesting ranges of *Calliope* species and their subspecies: *C. calliope* (1–*C. c. calliope*, 2–*C. c. beicki*), *C. pectoralis* (3–*C. p. tschebaiewi*, 4–*C. p. confuse*, 5–*C. p. pectoralis*, 6–*C. p. ballioni*), 7–*C. obscura*.

tering of a number of warbler species (Phylloscopidae) belonging to "alien" subgenera (Koblik et al., 2017).

The case of Audubon's warbler (Dendroica auduboni sensu stricto), which, as it turned out, is not just a southern group of subspecies of the myrtle warbler (D. coronata), but the product of its crossing with a presumably different species (Brelsford, 2011; Brelsford et al., 2011; Milá and Irwin, 2011), has been studied in the fauna of North America. The widespread morph auduboni has similarities with the myrtle warbler, the northern member of the parent pair. Nevertheless, the nature of its relationship with D. coronata sensu stricto (parapatria with narrow stable hybridization zones) does not correspond to the intergradation zones characteristic of subspecies (Hubbard, 1969), and this does not allow us to attribute the auduboni sensu stricto morph to the same species. By its coloration, it gravitates to isolated narrow-areal races nigrifrons and goldmani, possibly representing the "southern member of the pair." In the latest reports (del Hovo and Collar, 2016), the auduboni, nigrifrons, and goldmani morphs are combined under the senior name D. auduboni into a taxon of species rank (and partially hybridogenic origin). Some researchers (Milá and Irwin, 2011), in addition to recognizing the hybridogenic D. auduboni, consider the southern morphs as an independent species of *D. nigrifrons* or give a species rank to each of them.

A hypothesis was proposed for the origin of the Himalayan rubythroat (*Calliope pectoralis*) as a result of the long-standing hybridization of the Siberian rubythroat (*C. calliope*) and the blackthroat (*C. obscura*) (Spiridonova and Val'chuk, 2017; Spiridonova et al., 2019). The authors also assume the origin of the Tibetan rubythroat (*C. (c.) tschebaiewi*) during the later hybridization of *C. pectoralis* and *C. calliope*, interpreting the presence of a nuclear copy

BIOLOGY BULLETIN Vol. 47 No. 7 2020

of the mitochondrial genome of *C. calliope* in the "daughter" morph of *C. (c.) tschebaiewi*, and vice versa. The phenotypic characters and arealogical features of modern morphs were also taken into account (Fig. 1).

From the classical BCS, it follows that animal hybridization as a phenomenon is only a disruption of reproductive isolation (Mayr, 1968, 1974); therefore, it should not be considered as a factor of speciation. However, it has been shown in invertebrates that gene introgression can be a source of genetic variation for adaptation in new environmental conditions and can lead to rapid adaptive evolution (Lewontin and Birch, 1966), while hybrid species among animals (excluding higher vertebrates) are already in the hundreds (Bor-kin and Litvinchuk, 2013). The role of interspecific hybridization in the formation of the modern variety of birds remains essentially unexplored, largely due to the traditional rejection of such an opportunity by BCS supporters.

## MOLECULAR–GENETIC AND PHYLOGENETIC CRITERIA

Improving the methods for assessing the phylogenetic relationships of morphs makes it possible to use them more widely for the reconstruction of kinship within taxonomic complexes. Attempts are being made to estimate the approximate evolutionary age and relative timing of the isolation of specific taxa and their groups. Almost the entire modern version of PCS is essentially based on molecular research data. It is theoretically predicted that no later than the third decade of the 21st century, molecular studies will reliably justify the taxonomy of birds to a species level (Harr and Price, 2012). But the possibility of using various molecular genetic methods, as well as methods for constructing phylograms for assessing the kinship



Fig. 2. Probable pathways for the appearance of new haplotypes by reverse transfer of modified nuclear copies to the mitochondrial genome, according to Spiridonova et al., 2017 (with changes). (a) Phylogenetic network of mtDNA haplotypes of the cyt b C. calliope gene. Haplotype I [C. c. anadyrensis (2)-C. c. camtschatkensis (3)]; haplotype II [C. c. sachalinensis (4)]; haplotype III [C. c. calliope (1)]. Arrows between haplogroups indicate the past recombination event between nuclear copies of mtDNA (NUMT) and mtDNA, which resulted in a new haplotype. (b) Geographic distribution of mitochondrial C. calliope haplotypes over their range. The circle size displays the number of samples. The sector in the circle displays the representation of haplogroups: gray, haplogroup I; black, II; white, III. (c) Hypothetical diagram of the demographic history of the C. calliope subspecies, based on cyt b. Large arrows indicate the first stage of propagation; small arrows, the second. White arrows indicate haplogroup C. c. calliope; gray arrows, haplogroup C. c. anadyrensis-C. c. camtschatkensis. Rec I and Rec II are recombination events.

of various morphs, must be treated with great care (Pavlinov, 2005; Mayr, 2008; Wiley and Liberman, 2011; Pavlinov and Lyubarsky, 2011; Zelenkov, 2015).

In particular, the widespread use of mtDNA genes for the purpose of species identification (DNA coding) has led to the appearance of a number of "false species" in recent decades, as it turned out to be associated with nuclear copies of mitochondrial genes that co-amplify with orthologous mtDNA genes (Song et al., 2008). In some cases, significant differences in the mitochondrial markers used are leveled due to the ongoing hybridization between taxa or are the result of past gene exchanges, such as the yellowhammer (*Emberiza citrinella*) and pine bunting (*E. leucocephalos*) (Irvin et al., 2009).

The hypothesis of the possibility of the appearance of new haplotypes by the reverse transfer of modified nuclear copies to the mitochondrial genome (Spiridonova et al., 2016) explains well the cases of rapid emergence of sharp molecular genetic differences in very young population groups, which once again showed the inconsistency of using markers only of the mitochondrial genome. Thus, in the Siberian rubythroat (C. calliope) in northeastern Asia, the existence of two strongly isolated haplotype groups was found that correspond to the Far Eastern subspecies of clearly recent origin (Spiridonova et al., 2017). During the distribution of the species to northeastern Asia and Sakhalin, the event of homologous recombination probably occurred twice, entailing the exchange of a part of the mitochondrial genome for the corresponding nuclear copy, which significantly differs from the original version and was fixed in the colonized territories by the type of founder effect (Fig. 2). Significant divergence of mitochondrial haplotypes does not always indicate the antiquity of the groups, and, in accordance with the hypothesis mentioned above. may be a consequence of the recombination effect between parts of the nuclear genome and the mitochodrial genome. As in the case of the origin of the Himalayan rubythroat, the possibility of such a recombination appears controversial so far; however, this phenomenon is known or is assumed for other groups of living organisms (Potokina et al., 2017; Grebel'nyi et al., 2018).

Finally, an important point was the realization through systematics of the fact that deep or weak molecular differences do not always correspond to large or small phenotypic differences. There are cases when sympatrically living species are genetically indistinguishable by the markers traditionally used. For example, in a number of morphologically close, but reliably distinguishable species for which, under conditions of sympatric distribution, wide hybridization does not occur and/or strict assortativeness of pairing is proved, differences in mtDNA markers may be minimal or even absent. Such are the cases with representatives of the complex of North Palaearctic bullfinches (Pvrrhula pvrrhula, P. griseiventris, P. cineracea) (Arnaiz-Villena et al., 2001; Töpfer et al., 2011; Ivushkin, 2015) and three species of crossbills (Loxia curvirostra, L. scotica, L. pytyopsittacus) on the British Isles (Piertney et al., 2001; Summers et al., 2002, 2007). In turn, populations (not even geographic races) of the same species may have genetic differences corresponding to the usual distances between "good" species. Such, for example, are differences in mtDNA of two populations of the common redstart (*Phoenicurus* phoenicurus) from Germany, amounting to 5% (del Hoyo and Collar, 2014). The same species in different parts of the range may have a different set of mtDNAs (in regions of sympatry with a close species, it is often alien, borrowed as a result of hybridization), which, as has long been known, does not affect its phenotype and environmental characteristics (Vijay et al., 2016).

Almost all debatable, from the point of view of classical systematics, taxonomic decisions are the result of attempts to reconstruct phylogenetic relationships within particular groups based on the analysis of one or more individual mitochondrial or nuclear markers. Such an analysis, as a rule, is carried out without correlating the results of molecular genetic studies with elementary ideas about the morphological appearance of objects, their environmental specificity, and also without taking into account information about the nature of reproductive and spatial relationships between them.

It should be noted that in the systematization of complex near-species groups, including morphs of different evolutionary levels (from geographical races to good species), the relationships of which are complicated by cases of hybridization (and, as a result, the emergence of hybridogenic polymorphism), the use of the phylogenetic method remains the only means of reconstructing family ties, which is necessary for the correct taxonomic assessment of morphs (Red'kin et al., 2015). Ultimately, the most contradictory results of phylogenetic constructions can be correctly substantiated due to an integrated approach with the obligatory inclusion of phenotypic, ecological and morphological (in the broadest terms) and molecular genetic data with cross-checking the results (Abramson, 2013). This approach is called "integrative taxonomy" (Sangster, 2018).

## PHENOTYPIC AND OTHER "CLASSIC" CRITERIA

The traditional criteria for assessing the divergence level of disputed taxa, despite the well-known subjectivity, are used by ornithosystematics. Their set is even expanding due to the involvement in the analysis of not only morphological, but also behavioral, environmental differences, characteristics of vocalization, phenology, breeding biology, geographical location, and other aspects (Rasmussen and Anderton, 2005). For isolated morphs, the method is used with varying

BIOLOGY BULLETIN Vol. 47 No. 7 2020

degrees of success when the level of differences in a pair of allopatric taxa is estimated by comparing with the level of differences of close sympatric taxa with proven species status (Helbig et al., 2002).

In the framework of the recently proposed system of quantitative criteria for distinguishing species (Tobias et al., 2010), phenotypic differences (i.e., differences in plumage, morphology, morphometry, and vocalization) are evaluated on a four-point scale depending on their severity. Interdependent differences (for example, a longer wing and a proportionally larger beak) can only be evaluated once. In order to avoid exaggerating estimates of minor differences, only three coloring, two morphometric, and two acoustic differences can be evaluated. Molecular differences between taxa are not quantified because genetic and phenotypic differences are not correlated. Environmental and behavioral differences are also taken into account, and if they exist, they receive one extra point (or two points for "nonoverlapping differences in marital behavior"). Finally, the distribution features are taken into account: allopatric (no matter how strongly separated) areas do not give points at all, parapatria adds three points, a narrow hybridization zone adds two points, and a wide hybridization zone gives one point. Taxa that collect a total of seven or more points are considered distinct enough to obtain the status of full-fledged species (based on scores typed by similar sympatric species, and compared with lower scores for taxa that are generally recognized as subspecies). The Tobias Criteria are not used as a truly objective method, but rather are used as a practical tool to help assess the degree of difference between nonsympatric taxa in the most consistent way possible.

Despite the apparent obviousness and logic of the approach, it seems, in our opinion, unnecessarily "mechanistic." Its practical use, as a rule, leads to fragmentation of taxa; there are few cases of enlargement (del Hoyo and Collar, 2014, 2016). The "Tobias criteria" applied by us to the controversial taxa of bird fauna of Northern Eurasia almost always confirmed their species status.

## THE TERM "SPECIES" AS APPLIED TO BIRDS

Modern reviews (e.g., Kryukov, 2003; Coyne and Orr, 2004; Mallet, 2006; Price, 2008; Vasilyeva, 2009; Pavlinov and Lubarskii, 2011; Pavlinov, 2017, 2018, 2019; Rubtsov 2015; Sangster, 2018) interpret and evaluate the strengths and weaknesses of the main rival concepts of the species differently, as well as the evolutionary and phylogenetic paradigms, their ability to reflect the processes of speciation, and the applicability in taxonomy. Most reviews acknowledge that the concept of a species is not universal; in any case, the taxonomic and evolutionary entities of the category "species" should be distinguished. There are new definitions of the species. Supporters of BCS (Johnson et al., 1999) and supporters of PCS (Sangster, 2014) brought their positions closer, as a result of which the jointly developed "Integrated biological concept of species" was proposed: "A species in birds is a population system that is essentially monophyletic, genetically related, and genealogically matched related group of individuals that have the same breeding system in time and space, represent an independent evolutionary line and demonstrate a significant, but not necessarily complete reproductive isolation from other such systems" (del Hoyo and Collar, 2014). Thus, incomplete isolation and the presence of hybrids are not an obstacle to giving a species status to clearly distinguishable morphs that were previously considered conspecific.

Some domestic researchers doubt the fundamental possibility of a compromise between BCS and PCS. A.S. Rubtsov, not without reason, considers PCS an attempt to return to the typological concept of the species. He defines "the process of speciation as the establishment of sympatry between diverging taxa, and species as morphologically distinguishable groups of organisms that can coexist in the sympatry zone for a long time" (2015). However, based on this definition, we should not consider any parapatric taxa to be species, even if the impossibility of their sympatry and transboundary contacts is due to other factors, rather than the presence of introgressive hybridization.

Mikhailov (2003, 2015, 2017, 2018) considers the species as the smallest unit of morphogenetic resistance and the canalized reaction rate, i.e., as a result of various processes, not the continuum stage. In short terms, this is an epigenotype, i.e., dynamic archetype of morph implementation in a series of generations. Mikhailov considers only reproductive isolation as a marker of true species status, which is expressed in genetic incompatibility (post-copulative isolation) or due to interfering mating morphology, mismatch of odor signals, and other nonbehavioral parameters. On the other hand, he reduces the behavioral, precopulative isolation (so characteristic of birds and mammals) to a reversible assortativeness of mating based on the selectivity of preferences in pairing.

At the same time, it is not taken into account that the mismatch of the mating ritual in birds is no less (and sometimes more) an effective variant of reproductive isolation than, for example, the factor of reduced survival of hybrids due to genetic reasons. In other words, the emphasis is not on the degree of impact (effectiveness) of the insulating mechanisms, but only on their nature. Following this logic, we cannot establish the species status for sympatric cognate morphs, based only on the absence of visible hybridization in nature-it is necessary to establish each time what mechanisms impede it. Captive experiments can hardly be considered decisive, since animals are inevitably influenced by ex situ conditions (outside their natural habitats), and the reasons for the success/failure of breeding are difficult to assess quantitatively and qualitatively (Frankham, 2008). It is also unclear how the further divergence of the already noncrossing "behavioral" morphs occurs, which leads (under conditions of sympatry!) to the emergence of "true" morphoids, whether various morphoids are parapatric morphs without signs of hybridization, etc.

The appearance of behavioral precopulative isolation without concomitant postcopulative activity, in our opinion, can be considered an evolutionary breakthrough: the emergence of a factor that rather effectively (but not specifically) keeps the group from "erosion" and makes the existence of costly genetic, biochemical, and morphological barriers unnecessary provided a taxon achieves a high level of nervous activity. However, we do not exclude that behavioral precopulative isolation only marks the level of divergence, which is already accompanied by at least incomplete and implicit postcopulative isolation of morphs.

Based on practical tasks, we found it necessary to formulate such a definition of the species that it would more closely correspond to the current situation regarding birds and would be combined with the definitions of taxa of a lower rank. The definition proposed here is based on two leading criteria: biological, consisting in assessing the reproductive relationships of specific morphs with each other, and phylogenetic, assessing the degree of evolutionary relationship of taxa on both molecular-genetic and comparative morphological material.

A species is a complex of populations that has an evolutionary community (including morphological, genetic, environmental aspects) and is able to maintain its stability in contact with other species for a long time. The main criterion for the species, obviously, should be considered not the existing or potential limitations in hybridization, but its stability in time and space. It should be emphasized that maintaining stability implies not only reproductive isolation of different levels and different nature, but also other properties of populations in areas of contact: mutual avoidance (for example, divergence in ecological niches and stations, shift of reproductive cycles) and/or direct competition for resources with mutual exclusion. Not all species are able to live sympatrically, even in the absence of hybridization between them. In accordance with the theory of discontinuous equilibrium ("dotted evolution") of N. Eldridge and S. Gould (which received confirmation recently, Millien, 2006; Pagel et al., 2006), the stability of the species should be traced over a considerable period of time (from several thousand years), and for the time being hybrid species should not be considered full-fledged species, eco and socioraces that arose "before our eyes," even when they meet the criteria of the classic BCS (for example, as in the case of the "new" Galapagos finch).

It should be noted that our definition largely overlaps with the definition of the species in the evolutionary concept formulated by Wiley and Mayden (Wiley and Mayden, 1985) based on the views of J. Simpson: "A species is a biological object consisting of organisms that preserves its individuality in time and space, and having its own evolutionary fate and historical trends." However, it is more detailed and does not contain fuzzy statements regarding "fate" and "trends." We believe that it is inevitable to use the PCS criteria in the analysis of taxa with allopatric distribution, in the detection of hybridogenic polymorphism, and in other complex cases (Red'kin et al., 2015, 2016).

The genome of almost any species includes foreign DNA, indicating, inter alia, periodic hybridization with other species (Hailer et al., 2012; Miller et al., 2012; Soubrier et al., 2016). Nevertheless, even with a significant admixture of a foreign genome, the species retains its ecological and morphological specificity for a long time (probably, until the period of "imbalance" caused by various reasons).

## THE CONCEPT OF "SUBSPECIES"

The term "subspecies" is often mistakenly used as an antithesis to the concept of "species," in the meaning of "taxon that has not reached species independence," "non-species." The concept of "subspecies" was finally legalized in the second half of the 19<sup>th</sup> century to denote units of intraspecific geographical variability (Vinarskii, 2015) and is currently the smallest taxonomic category regulated by the International Code of Zoological Nomenclature (2004). The main approach studying the geographical variability of a species historically came down to a description of the external morphological differences of one group of individuals geographically remote from another group of individuals of the same species and its nomenclature designation.

For all subspecies, a nomenclature designation with a hierarchical (genus, species, subspecies) trinomial name is used. The criteria for isolating a subspecies are stable morphological differences, often with minimal differences in the ecological features, or lack thereof. Oddly enough, the term "subspecies" continues to be very vague, in view of the different meanings attached to it (Vinarskii, 2015). There even exists a tendency to avoid the word "subspecies," replacing it with the synonyms "race." or "variety." "Varieties differ in a few, purely superficial characters, whereas species differ in many interdependent properties" (Panov, 1993).

The manifestation of geographical variability of external morphological characters is characteristic of the vast majority of animals. Most frequently, such variability is expressed in the formation of geographical races, to a greater or lesser extent reflecting the population structure of species. Geographic races can be both sharply differentiated (but to a lesser extent than species within a given genus or subgenus) and relatively weakly (but statistically significantly) distinguishable (Red'kin and Konovalova, 2006). The polytypic species may include races of different ages: from recently isolated but having significant differences (fixed due to the founder's effect) to relict ones that have existed for a long time under conditions of reliable spatial isolation, but in some cases entering into intergradation. In the contact points (if one takes place) of the corresponding morphologically isolated populations (or their groups), transition zones intergradation zones (or regions of unlimited mixing of characters)—are formed. The width of such zones varies significantly, but it is always less than the area of the regions occupied by "phenotypically pure" populations, i.e., areas within which the morphological characters of the corresponding subspecies are stable.

Clinal (geographical) variability is accepted by us, following many authorities, as a gradual change in one or more morphological characters at a considerable distance within a geographical continuum of populations of this species. Within this continuum, it is almost impossible to distinguish zones in which these signs become stable. Among the birds of the Palaearctic fauna, cases of clinal variation are objectively rare and poorly understood. As an example, the color variation of plumage in the great reed warbler (Acrocephalus arundinaceus), expressed in the gradual lightening of the general color from west to east, can be cited. Researchers tried to isolate the eastern populations of this species into the subspecies "A. a. zarudnyi" (Dementiev, 1937; Vaurie, 1959; Portenko, 1960). However, this point of view does not find confirmation due to the inability to outline areas of the constancy of manifestation of color differences (Opaev, 2010). In some cases, within a very widespread subspecies, for example, the long-tailed tit (Aegithalos caudatus caudatus), the variability of a number of dimensional characters from Scandinavia to the coast of the Sea of Okhotsk can be of a fluctuating nature, without significant differences between neighboring geographical samples (Lukyanchuk et al., 2017).

In many cases, the researchers who conducted the revision of the subspecific taxonomy failed to reach consensus on a number of geographic races of a species. Taxonomic decisions were often made by experts based on a study of easily available collection materials. However, the materials distributed across museum collections are extremely uneven and sometimes do not reflect the real picture of geographical variability. One of the reasons for the inconsistencies arising is that researchers who revise species are not able to process numerous but scattered materials with the same degree of detail (Red'kin, 2015).

Phylogeographic studies are currently positioned as one of the main directions in understanding the population genetic structure of species and the effect of hybridization in the contact zones of related taxa (Politov and Mudrik, 2018). However, the picture revealed as a result of such studies of polytypic bird species, in most cases, does not coincide with traditional ideas about the geographical variability and intraspecific taxonomy of these groups.

Usually, a direct relationship between haplogroups and geographical races is observed in species that are extremely weakly susceptible to geographical variability. Such, for example, is the rook (*Corvus frugilegus*), the isolation of two well-defined subspecies of which is clearly supported by phylogeographic constructions. In general, the phylogeographic structure of a species, revealed by mtDNA analysis methods, extremely rarely reflects the geographical variability of morphological characters of birds (Haring et al., 2007), which gives phylogeographers grounds to accuse morphologists of the "phantom nature" of a number of subspecies (Zink, 2004).

For all widespread polytypic species, the presence of phylogeographic structures marking groups or races can be traced only in separate parts of the breeding range, while in most of it the isolation of local morphs is completely undetected by such techniques. Thus, the reliably geographically isolated Kamchatka magpie race (*Pica pica camtschatica*) is sharply distinguished by molecular markers from six other races of the "western" group in contact with each other and not having phylogeographic differences (Kryukov et al., 2017).

The emergence of geographic races can occur in just a few decades. For example, in the populations of the introduced red-whiskered bulbul (Pycnonotus *jocosus*) formed on the islands of Reunion, Mauritius, and Oahu, noticeable morphological differences from the ancestral populations have appeared. Moreover, over 30 years, two populations with genetic differences formed on Renion (Le Gros et al., 2016). For the silvereye (Zosterops lateralis), which quickly settled on islands near Australia, it was shown that an increase in the size of the body of the island morphs took place over only 200 years. Moreover, the dimensions of the morph Z. l. chlorocephalus that arose during this time on Heron Island exceed the size of its mainland ancestor Z. l. familiaris by almost one-third (Clegg et al., 2002).

In some cases, the occurrence of traits marking differences in population groups is caused by past or currently occurring interspecific hybridization. Vivid examples of such morphs are the eastern yellowhammer (*Emberiza citrinella erythrogenys*) (Panov 1989, 2001), western yellow wagtail (*Motacilla flava thunbergi*) (Red'kin, 2001a, 2001b; Sotnikov, 2006), and the Turkestan shrike (*Lanius phoenicuroides karelini*, 2008).

In our opinion, any geographic morphs of a species that are statistically significantly different in morphological characters, regardless of their evolutionary age, should be qualified as subspecies as a taxonomic category. The description of the new subspecies (with their nomenclature designation) seems appropriate for the degree of fragmentation at which they will most fully reflect the geographical (population) structure of this species. Researchers usually either ignore populations/morphs of hybridogenic origin (proven or presumed) in terms of nomenclature designation (in which case their names are given in quotation marks), or they do not distinguish among other subspecies names. In our opinion, such morphs, if they meet the criteria for distinguishing geographical races, should be denoted by a trinomial name, accompanied by some icon (for example, an asterisk, *Emberiza citrinella erythrogenys\**), which is not regulated by the Code, but which directly indicates the hybridogenic origin of the taxon.

It is wrong to consider any subspecies as a potential species. A geographic race is able to reach the species level of divergence only under the condition of prolonged isolation in the refugium. However, in the classical PCS there is simply "no place left" for BKV subspecies: these taxa obtain the rank of species (Vinarskii, 2015, 2015a).

We define a subspecies as follows: A subspecies (=geographic race) is a population or group of populations of a species that has stable morphological differences from neighboring populations, but can freely cross with them in contact areas (if any) with the formation of transition zones (intergradation zones). The sympatry of subspecies without the formation of zones of integradation in birds is almost impossible. The absence of reproductive isolation is also expected between representatives of geographically isolated subspecies classified as a common species on the basis of morphological (sometimes genetic) data.

Interesting exceptions (with respect to sympatry of conspecific morphs) are situations with the so-called ecological races, studied for the red crossbill (Loxia *curvirostra*). In the North American populations of this species, nine ecological races are distinguished (Parchman et al., 2006); another seven such races are known for Western European populations (Edelaar et al., 2008). These races are similar in song structure, but clearly distinguishable by their calls and, being adapted to feeding on different species of conifers, differ in several morphometric characters, primarily in the structure of the beak. It is believed that the divergence of ecological races began no earlier than 11000 years ago, with the advent of the modern postglacial era (Benkman et al., 2010). This conclusion is consistent with the data of molecular studies: ecological species of crossbills do not differ in mtDNA, but demonstrate stable differences in series by multilocus markers. Outside the breeding season, crossbills form nomadic flocks, each flock consists of individuals of only one ecological race (while all members of the flock issue only one type of call), and mating pairs form between members of the same flock. If you strictly follow the criteria of BCS, the red crossbill eco-species can be interpreted as "independent species in the early stages of divergence" (Edelaar, 2008)

and regarded as possible evidence of sympatric speciation in birds. However, taking into account the nomadic nature of nests and roosters of crossbills (typical of many true finches), we assume that eco-species formed allopatrically and their sympatry arose as a secondary phenomenon, as a result of nomadic migrations caused by yields and crop failures of seeds of specific conifers. In our opinion, they can be considered the equivalent of normal geographic races and can be designated as subspecies, since in the conditions of periodic reduction of food resources, the reproductive isolation between them can be violated, leading to the exchange of genes and, possibly, merging with each other.

## THE CONCEPT OF "SEMISPECIES"

The term "semispecies" was introduced by E. Mayr in 1942 (Mayr, 1942). According to his definition, "Morphs at the final stages of divergence are designated in the framework of BCS by the term "semispecies," which means closely related taxa that have reached the species level of divergence, but whose species status cannot be confirmed due to their allopatric distribution or due to incomplete reproductive isolation. Unlike subspecies, semispecies have partially formed insulating mechanisms, so hybridization between them does not have the nature of introgression and does not lead to their merging" (Mayr, 1968).

At the time of the emergence of BCS, many possibilities for assessing the level of isolation of taxa, which we now have, were absent, so almost all hybridizing and all morphologically similar allopatrically distributed slightly related species automatically fell into the concept of semispecies. A variety of assessments of the phenomenon of semispecies is still observed today: from the proposal to consider semispecies as one of the mandatory steps of lower-rank taxa (Pfander, 2018) to completely denying the biological meaning of this concept and its interpretation as a buffer category ("waste bin") for morphs with unexplored family ties and reproductive relationships (Mikhailov, 2018). The concept of semispecies (allospecies) was actively used by Stepanyan (1983), dividing supraspecific complexes into the categories of superspecies and ex-conspecies. Rubtsov also uses the concept of semispecies (2015). Theriologists (Pavlinov, 2019) currently prefer the term allospecies.

The identification of the border taxonomic category "semispecies" is not specifically regulated by the Code of Zoological Nomenclature (2004). Thus, any morphs the rank of which is deemed to be higher than subspecies can be equated with species and appear further under binomial Latin names, for example, in environmental regulatory documents. However, in our opinion, when compiling avifauna lists, as well as in special works devoted to the evolution and taxonomy of taxonomic groups, the use of this category seems quite justified, since these are still not species in the full sense of the word. In our interpretation, a "semispecies" is a population or a number of populations that does not meet the concept of a species according to all the criteria, but has more significant differences with neighboring populations than subspecies and is able to form sympatric zones with them without intergradation into them. In all cases, semispecies are young, but already very isolated morphs (or groupings of morphs), showing incomplete reproductive isolation in contact with close morphs.

For the semispecies that make up one superspecies, parapatric distribution is most typical. If the close boundaries of their ranges are not set by natural linear barriers (riverbeds, ridges, etc.), the parapatria of such morphs often appears as follows: narrow zones of spatial contact are interspersed with gaps, where both members of the pair are absent, or have a mosaic focal distribution with low numbers. Spatial relations of this kind are characteristic, for example, of the yellowbrowed warbler (Phylloscopus (inornatus) inornatus/Ph. (inornatus) humei) (Red'kin and Konovalova, 2003, 2004) or the Siberian stonechat (Saxicola (torguata) maura/S. (torguata) stejnegeri) (Opaev et al., 2018). In the areas of direct contact of semispecies, no zones of intergradation characteristic of geographical races of the same species are formed (Kryukov and Blinov, 1981; Blinov et al., 1993; Marova and Shipilina, 2015). The presence of gaps and the focal nature of distribution are also explainable: diverging in terms of habitat requirements more than geographical races, semispecies at the edges of habitats can be in pessimal (suboptimal) conditions. This circumstance does not allow semispecies to populate a "controversial" space with a normal density characteristic of populations of a single species.

An example of parapatric distribution is two polytypic Carduelis complexes: the goldfinch (Carduelis (carduelis) carduelis) and the Eastern grav-headed goldfinch (C. (carduelis) caniceps). They are characterized by a narrow zone of spatial contact in which constant hybridization exists, but it does not lead to the formation of populations with transitional characters (Zablotskaya, 1975). The phylogenetic differences between these morphs are also minimal (Arnaiz-Villena et al., 2001). The morphological differences between the representatives of these complexes are deep and affect many coloring and plastic characters. There are steady differences in the voice, including differences in the structure of the calls. In the Russian ornithological literature, complexes are traditionally interpreted as species, in the foreign "post-Mayrovian" literature as conspecific forms, however, in the latest edition of Illustrated Checklist of the Birds of the World (del Hoyo and Collar, 2016), they already appear as independent species. In the interpretation proposed in this paper, the goldfinch and gray-headed goldfinch are undoubted semispecies.

There are many cases when the controversial morphs form vast zones of sympatry. An example is

the complex of North Palaearctic bullfinches, in which two geographically separated morphs are represented: the common (Pyrrhula (pyrrhula) pyrrhula) and Far Eastern (P. (pyrrhula) griseiventris) bullfinches, as well as the Baikal bullfinch (P. (pyrrhula) *cineracea*), which is sympatric to two other morphs. In the foreign literature, all these morphs are considered conspecific only because they are extremely close genetically (Arnaiz-Villena et al., 2001). However, the fact of sympatry with extremely rare hybridization contradicts this interpretation. In addition to coloring, birds of the three morphs differ from each other in size and proportions, and there are quite audible differences in voice (Ivushkin, 2015). Thus, with objective genetic proximity, these morphs cannot be accepted only as geographical races. In similar cases with taxonomic pairs, red-throated/black-throated thrushes (Turdus (ruficollis) ruficollis/T. (ruficollis) atrogularis) and Naumann's/dusky thrushes (T. (naumanni) naumanni/T. (naumanni) eunomus), the members of which have also been considered for a long time conspecific geographical races in the presence of broad sympatry, it is now customary to consider them as independent species (Stepanyan, 2003; Dickinson and Christidis, 2014; del Hoyo and Collar, 2016; Clements, 2017; etc.), despite regular hybridization (Portenko, 1981; Val'chuk et al., 2013). Based on our views (Red'kin et al., 2015), both the bullfinches mentioned and the thrushes mentioned are semispecies.

The vellow-headed wagtail (*Motacilla* (*flava*) *lutea*) is a morph that is considered in foreign reports only as a subspecies of the western yellow wagtail (Motacilla *flava* sensu stricto) and is distributed sympatrically with the *conspecific M. f. flava* and *M. f. beema* almost throughout its range, from the Volga region to the southern part of Western Siberia and northern Kazakhstan. This contradicts the conventional wisdom on geographic races. In addition, in the south, part of its nesting area overlaps with the range of the black-headed wagtail (M. (flava) feldegg). From the sympatrically distributed races of the yellow and black-headed wagtail, the yellow-headed one differs sharply in the coloration of males, biological features, and ecological preferences (Bakhtadze and Kazakov, 1985; Bakhtadze, 1987; Murav'ev, 1993, 1996, 1997). Based on the presence of sympatry in the absence of visible introgressive hybridization, Stepanyan (1978, 1983, 2003) gave this morph the status of a monotypic species (although he included the allopatric North Atlantic morph flavissima). In our opinion, based on the current situation, it is more correct to qualify the lutea morph (but without the phenotypically similar flavissima) as a semispecies, since it is neither a stable species, nor, moreover, a geographical race.

It is rather difficult to qualify allopatrically common related morphs as semispecies (allospecies in the narrow sense). Without experiments in captivity (sometimes yielding mixed results), we cannot judge the degree/absence of reproductive isolation in the compared populations; the genetic distances currently known, like phenotypic differences, are not a universal criterion (see above). Nevertheless, in cases where the entire supraspecific complex is considered (including sympatric and parapatric morphs), it is possible to draw conclusions about the status of its allopatric members. In particular, this is shown in relation to the already mentioned supraspecies of the African stonechat (*Saxicola torquata* sensu lato), including its poorly studied isolated morph (semispecies), the Siberian stonechat (*S. (torquata) przewalskii*) (Kalinin et al., 2018).

As part of the same supraspecific complexes in the status of semispecies, both morphs that can easily be diagnosed using molecular genetic markers and morphs the genetic differences of which are leveled due to current or past hybridization can be taken. An example is the group *Remiz pendulinus* sensu lato, in which the white-crowned penduline tit (R. (*pendulinus*) and the Chinese penduline tit (R. (*pendulinus*) consobrinus) are genetically well differentiated, while the morphologically and ecologically sharply isolated from each other Eurasian penduline tit (R. (*pendulinus*) *pendulinus*) are practically indistinguishable genetically (Barani-Beiranvand et al., 2017).

Phenotypically similar, but phylogenetically distant, not closely related morphs or groupings of morphs cannot be considered as semispecies even in cases when regular hybridization takes place between their representatives, such as between the phenotypically similar great reed warbler (*Acrocephalus arundinaceus*) and the clamorous reed warbler (*A. stentoreus*) or between the herring gull (*Larus argentatus*) and the Caspian gull (*L. cachinnans*).

We admit that, not having acquired sufficiently effective reproductive isolation, but already having left refugia, semispecies may again merge with each other due to introgressive hybridization. The "unbalanced" form in the future can be entirely absorbed by the more numerous and stable one or several related forms. Such a development of events probably takes place in the case of the western yellow wagtail (*Motacilla (flava) lutea*), which has already disappeared over most of the nesting range in Asia during literally the last 100 years of observations, where there are only a few individuals with traces of crossing with a yellow wagtail (Red'kin, 2012; Ryabitsev, 2014).

Most forms that meet the definition of a semispecies, at the moment, do not show obvious tendencies to secondary fusion or "dissolution" in another form. In order to characterize with certainty the course and outcome of these processes, hundreds (possibly thousands) of years of observation are needed.

The issue of nomenclature designation of semispecies has not yet been resolved, in part due to the vagueness of the concept itself, which is not recognized by

No.	Taxonomic status	Ecological segregation/ assortative mating	Development of the situation in the secondary contact zone
1a	Ecological races	Present/present	With a sharp reduction in resources, the mechanisms
			of precopulation isolation are disrupted. Mass hybridization
			in the absence of spatial isolation between diverging taxa leads
			to their complete merger
1b	Subspecies	Absent/absent	Mass hybridization in a gradually expanding contact zone will lead
			to the fusion of taxa over time
1c	Subspecies	Present/absent	The same as 1b, but the expansion of the contact zone and the
			merging of taxa occurs faster (Grabovskii, 1995)
Lower boundary of a species			
2a	Semispecies	Absent/present	The formation of a narrow and time-stable zone of secondary
			contact
2b	Semispecies	Present/present	Formation of a wide contact zone, random hybridization. If hybrids
			are more competitive in the choice of habitats than their parental
			forms, the level of hybridization gradually increases and ecological
			segregation between diverging taxa disappears, which leads
			to a reduction in the contact zone and the establishment
			of a narrow and time-stable hybrid zone
Upper boundary of a species			
3	Sister species	Present/present	If hybrids are less competitive when choosing habitats than parent
			forms, then the level of hybridization remains low. A wide zone
			of sympatry is formed

 Table 1. Stage of speciation and substantiation of the reality of species (Rubtsov, 2015)

many taxonomists. Ideally, the continuum of stages of the speciation process from a "well-separated race/subspecies group" to "almost a species" (ex-conspecies in the interpretation of Stepanyan, 1983) requires a fractional hierarchy with several additional gradations between the subspecies and species ranks. It seems useful at least to introduce the single designation of semispecies as a special additional category. In the ornithological reports of recent years, semispecies appearing under binomial names make up the "lion's share" of the hundreds of "new species" that caused irritation and accusations of ornithosystematics of excessive fragmentation and abandonment of BKV. But the same semispecies are "masked" in the bulletins as groups of subspecies, conveniently labeled with different colors (del Hoyo and Collar, 2014, 2016). We believe that it is most correct (Koblik et al., 2006; Koblik and Arkhipov, 2014; Red'kin et al., 2015; etc.) to use binomial Latin names for all semispecies with the obligatory designation of their belonging to a specific species group (subspecies). The International Code of Zoological Nomenclature (2004) allows the use of the older name in parentheses between the name of the generic group and the species name to designate a species group (Article 6, "Intercalar Names," paragraph 2). Such a designation, for example, Parus (major) bokharensis, clearly shows the difference between the taxon and the species, as well as the geographical race.

Considering, following Mayr (1968, 1971) and Stepanyan (1983), geographical variability and speciation as

BIOLOGY BULLETIN Vol. 47 No. 7 2020

slightly different phenomena, we believe that semispecies (even those in the early stages of formation) should appear in summaries and catalogs in species lists (indicating the superspecies in brackets), and not in the lists of subspecies within species "in a broad sense."

At the current level of our knowledge, none of the groups of species criteria can claim universality. Given the inevitable eclecticism and subjectivity of an integrated approach ("integrative taxonomy"), so far only such an assessment of various characters allows making adequate decisions in borderline speciation situations in birds.

Recognizing the problem of "non-universality" of interpretations, we, nevertheless, tried to give the three concepts in birds in interrelation: species, subspecies, and semispecies, for the first time, having formulated them taking into account the practical application of the data and concepts that have appeared in recent decades. Rubtsov (2015), in a theoretical work conceptually close to our views, "Reproductive Isolation and the Concept of Species in Birds," gives the stages of speciation with the characteristics of situations in contact zones in the form of a table. The stages distinguished by him and the corresponding options for giving status to the forms located at these stages, in general terms, correspond to the concepts we are proposing, including the concept of a semispecies as a taxon that is on the path of evolution into an independent species (Table 1).

According to our estimates, the avifauna of Russia and adjacent territories contains at least 40 semispe-



Fig. 3. Names of lower taxa in the biological concept of the species. The upper part of the diagram shows the spatial contact between taxa, and the lower one shows the boundaries of the corresponding species within different concepts. (1) Species group; (2) zoogeographic species-subspecies; (3) zoogeographic species-isospecies (independent species); (4) parapatric species; (5) a group of subspecies, megapods; (6) subspecies; (7) wide (over 100 km) intergradation zone; (8) narrow hybrid zone; (9) zone of parapatric contact; (10) wide overlap of areas; (11) phylogenetic species (PCS); (12) evolutionary species; (13) biological species (BCS); (14) zoogeographic species. In this example, 5, 4, 3, or 2 taxonomic species are recognized depending on which concept of the species is used and where the corresponding species boundary is established (Haffer, 1997).

cies that make up the core of controversial taxonomic cases in this region (Red'kin et al., 2015). Our solution, the regulation of the concept of "semispecies" within the framework of the widely interpreted BKV and the introduction of semispecies as an additional category, allows, without going beyond the requirements of the taxonomic nomenclature, to indicate the continuity of the process of evolution of species. Most of the weakly differentiated "species," the isolation of which in recent decades has led to accusations of excessive fragmentation, should apparently be regarded as semispecies.

The proposal to introduce the concept of "semispecies" into normal taxonomic usage as an intermediate category, reflecting the incomplete

stages of the speciation process, from our point of view, does not contradict the biological and evolutionary concepts of the species (semispecies fill the hiatus between them). From the standpoint of typological and phylogenetic concepts of a species, semispecies should be considered full-fledged species, and from the standpoint of the zoogeographic concept of a species, they should not be considered as such (Fig. 3).

We are aware that the solution of the "species problem" in a philosophical manner can be carried out in a variety of ways, including a flexible, virtually "rankless" phylogeographic approach (Pavlinov, 2018). Perhaps our definitions and solutions may seem to some to be suboptimal, private, and conservative. Nevertheless, in our experience, they work best in practice in assessing disputed and borderline situations among birds within the framework of generally accepted approaches in taxonomy and scientific nomenclature.

## ACKNOWLEDGMENTS

We are sincerely grateful to M.N. Dement'ev for the excellent translation of the preface in the *HBW and BirdLife International Illustrated Checklist of the Birds of the World* (del Hoyo and Collar, 2014), which greatly facilitated our work; K.E. Mikhailov for numerous long discussions on the "species issue," which allowed us to understand a lot for ourselves; and A.A. Lisovskii and K.V. Makarov for valuable comments and criticism at the stages of preparing both the manuscript of the article and the abstract of the report at the 1st All-Russia Ornithological Congress (Tver, January 29–February 4, 2018).

#### COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

## REFERENCES

Abramson, N.I., Molecular and conventional phylogenetics: on the way to mutual understanding, in *Sovremennye problemy biologicheskoi sistematiki* (Modern Problems of Biological Taxonomy), Tr. Zool. Inst. Ross. Akad. Nauk, Pril., 2013, pp. 219–229.

Arnaiz-Villena, A., Guillen, J., Ruiz-del-Valle, V., Lowy, E., Zamora, J., Varela, P., Stefani, D., and Allende, L.M., Phylogeography of crossbills, bullfinches, grosbeaks, and rosefinches, *Cell. Mol. Life Sci.*, 2001, vol. 58, pp. 1–8.

Aver'yanov, A.O. and Lopatin, A.V., Macrosystematics of placental mammals: the current state of the problem, *Zool. Zh.*, 2014, vol. 97, no. 7, pp. 798–813.

Bakhtadze, G.B., Distribution of pigments in feathers of yellow wagtails (*Motacilla flava* L., *M. feldegg* Mich., and *M. lutea* Gmel.) and their feathering color, *Izv. Sev.-Ka-vkaz. Nauchn. Tsentra Vyssh. Shk., Ser. Estestv. Nauki*, 1987,

Rostov-on-Don, deposited at VINITI August 18, 1987, no. 1920.

Bakhtadze, G.B. and Kazakov, B.A., Comparative analysis of nesting places of *Motacilla flava*, *M. feldegg*, and *M. lutea* yellow wagtails in the south of the European part of the USSR, *Vestn. Zool.*, 1985, no. 5, pp. 55–59.

Barani-Beiranvand, H., Aliabadian, M., Irestedt, M., Qu, Y., Darvish, J., Szekely, T., van Dijk, R.E., and Ericson, P.G.P., Phylogeny of penduline tits inferred from mitochondrial and microsatellite genotyping, *J. Avian Biol.*, 2017, vol. 48, pp. 932–940.

Barrera-Guzman, A.O., Aleixo, A., Shawkey, M.D., and Weir, J.T., Hybrid speciation leads to novel male secondary sexual ornamentation of an Amazonian bird, *Proc. Natl. Acad. Sci. U. S. A.*, 2017, vol. 115, pp. e218–e225. https://doi.org/10.1073/pnas.1717319115

Becker, J., Nachtigallen *Luscinia megarhynchos*, Sprosser *L. luscinia* und ihre Hybriden im Raum Frankfurt (Oder) weitere Ergebnisse einer langjahrigen Beringungsstudie, *Vogelwarte*, 2007, vol. 45, no. 1, pp. 15–26.

Benkman, C.W., Parchman, T.L., and Mezquida, E.T., Patterns of coevolution in the adaptive radiation of crossbills, *Ann. N.Y. Acad. Sci.*, 2010, vol. 1206, pp. 1–16.

Blinov, V.N., Blinova, T.K., and Kryukov, A.P., Interaction of hooded crow and carrion crow (*Corvus cornix* L. and *C. corone* L.) in the hybridization and sympatry zone: zone structure and possible isolation factors, in *Gibridizatsiya i problema vida u pozvonochnykh* (Hybridization and the Species Problem in Vertebrates), Trudy Zool. Muz. Mosk. Gos. Univ., 1993, vol. 30, pp. 97–117.

Borkin, L.Ya. and Litvinchuk, S.N., Hybridization, speciation, and taxonomy of animals, in *Sovremennye problemy biologicheskoi sistematiki* (Modern Problems of Biological Taxonomy), Tr. Zool. Inst. Ross. Akad. Nauk, 2013, suppl. 2, pp. 83–139.

Brelsford, A., Hybrid speciation in birds: allopatry more important than ecology?, *Mol. Ecol.*, 2011, vol. 20, pp. 3705–3707.

https://doi.org/10.1111/j.1365-294X.2011.05230.x

Brelsford, A., Milá, B., and Irwin, D.E., Hybrid origin of Audubon's warbler, *Mol. Ecol.*, 2011, vol. 20, no. 11, pp. 2380–2389.

Clegg, S.M., Degnan, S.M., Moritz, C., Estoup, A., Kikkawa, J., and Owens, I.P., Microevolution in island forms: the roles of drift and directional selection in morphological divergence of a passerine bird, *Evolution*, 2002, vol. 56, no. 10, pp. 2090–2099.

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L., and Wood, C.L., Clements checklist of birds of the world, 2017. http://www.birds.cor-nell.edu/clementschecklist.

Coyne, J.A. and Orr, H.A., *Speciation*, Sinauer Associates, 2004.

Dement'ev, G.P., *Polnyi opredelitel' ptits SSSR: Vorob'inye* (Complete Identification Guide to Birds of the USSR: Passeriformes), Moscow, 1937, vol. 4.

Edelaar, P., Van Eerde, K., and Terpstra, K., Is the nominate subspecies of the common crossbill *Loxia c. curvirostra* 

BIOLOGY BULLETIN Vol. 47 No. 7 2020

polytypic? II. Differentiation among vocal types in functional traits, *J. Avian Biol.*, 2008, vol. 39, pp. 108–115.

Frankham, R., Genetic adaptation to captivity in species conservation programs, *Mol. Ecol.*, 2008, vol. 17, no. 1, pp. 325–333.

Garnett, S.T. and Christidis, L., Taxonomy anarchy hampers conservation. The classification of complex organisms is in chaos, *Nature*, 2017, no. 546, pp. 25–27.

Grebel'nyi, S.D., Ivanova, N.Yu., and Nefedova, E.A., Exchange between the nuclear and mitochondrial genomes (according to the analysis of nuclear and cytoplasmic copies of mitochondrial genes—*numts* and *cymts*)), *Tsitologiya*, 2018, vol. 60, no. 11, pp. 899–902.

Le Gros, A., Clergeau, Ph., Zuccon, D., Cornette, R., Mathys, B., and Samadi, S., Invasion history and demographic processes associated with rapid morphological changes in the red-whiskered bulbul established on tropical islands, *Mol. Ecol.*, 2016, vol. 25, no. 21, pp. 5359–5376.

Haffer J., The history of species concepts and species limits in ornithology, in *Avian Systematics and Taxonomy*, Monk, J.F., Ed., *Bull. British Ornithologists Club. Centenary Supplement*, 1992, vol. 112A, pp. 107–158.

Haffer, J., Species concepts and species limits in ornithology, in *Handbook of the Birds of the World*, vol. 4: *Sandgrouse to Cuckoos*, del Hoyo, J., Elliot, A., and Sargatal, J., Eds., Lynx, 1997, pp. 11–24.

Hailer, F., Kutschera, V.E., Hallstrom, B.M., Klassert, D., Fain, S.R., Leonard, J.A., Arnason, U., and Janke, A., Nuclear genomic sequences reveal that polar bears are an old and distinct bear lineage, *Science*, 2012, vol. 336, no. 6079, pp. 344–357.

https://doi.org/10.1126/science.1216424

Haring, E., Gamauf, A., and Kryukov, A., Phylogeographic patterns in widespread corvid birds, *Mol. Phylogenet*. *Evol.*, 2007, vol. 45, no. 3, pp. 840–862.

Harr, B. and Price, T., Speciation: clash of the genomes, *Curr. Biol.*, 2012, vol. 22, no. 24, pp. R1044–R1046. https://doi.org/10.1016/j.cub.2012.11.005

Helbig, A.J., Knox, A.G., Parkin, D.T., Sangster, G., and Collinson, J.M., Guidelines for assigning species rank, *Ibis*, 2002, vol. 144, no. 3, pp. 518–525.

*HBW and BirdLife International Illustrated Checklist of the Birds of the World*, vol. 1: *Non-passerines*, del Hoyo, J. and Collar, N.J., Eds., Lynx, 2014.

HBW and BirdLife International Illustrated Checklist of the Birds of the World, vol. 2: Passerines, del Hoyo, J. and Collar, N.J., Eds., Lynx, 2016.

Hubbard, J.P., The relationships and evolution of *Dendroica coronata* complex, *Auk*, 1969, vol. 86, pp. 393–432.

Irwin, D.E., Rubtsov, A.S., and Panov, E.N., Mitochondrial introgression and replacement between yellowhammers (*Emberiza citrinella*) and pine buntings (*Emberiza leucocephalos*) (Aves: Passeriformes), *Biol. J. Linn. Soc.*, 2009, vol. 98, pp. 422–438.

Ivushkin, V.E., Genus *Pyrrhula* Brisson, 1760: composition, distribution, and features of ecology, *Russ. Ornitol. Zh.*, 2015, vol. 24, no. 1143, pp. 1679–1738.

Johnson, N.K., Remsen, J.V., and Cicero, C., Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept, in *Proceedings of the 22nd International Ornithological Congress, Durban, South Africa, August 1998*, Adams, N.J. and Slotow, R.H., Eds., Johannesburg, 1999, pp. 1470–1482.

Kalinin, E.D., Opaev, A.S., Solov'eva, E.N., Golovina, M.V., Marova, I.M., and Redkin, Ya.A., A comprehensive analysis of the variability of Palaearctic forms of European stonechats, in *Vseross. ornitol. kongr. (g. Tver', Rossiya,* 29 yanvarya–4 fevralya 2018). Tezisy dokladov (All-Russia Ornithological Congress (Tver, Russia, January 29–February 4, 2018), Abstracts of Papers), Tver, 2018, pp. 139–140.

Koblik, E.A. and Arkhipov, V.Yu., Avifauna of countries of Northern Eurasia within the former Soviet Union, in *Zoo-logicheskie issledovaniya* (Zoological Research), Moscow, 2014, no. 14.

Koblik, E.A., Redkin, Ya.A., and Arkhipov, V.Yu., *Spisok ptits Rossiiskoi Federatsii* (Checklist of Birds of the Russian Federation), Moscow, 2006.

Koblik, E.A., Arkhipov, V.Yu., Volkov, S.V., Mosalov, A.A., and Redkin, Ya.A., Himalayas—the "key" to understanding the taxonomic diversity of Asian warblers (Phylloscopidae, Aves), in *Rossiiskie gimalaiskie issledovaniya: vchera, segodnya, zavtra* (Russian Himalayan Studies: Yesterday, Today, and Tomorrow), St. Petersburg, 2017, pp. 173–178.

Kováts, D., Végvári, Z., and Varga, Z., Morphological patterns of a nightingale population in a contact zone of *Luscinia megarhynchos* and *L. luscinia, Acta Zoologica Academiae Scientiarum Hungaricae*, 2013, vol. 59, no. 2, pp. 157– 170.

Kryukov, A.P., Modern concepts of the species and the role of Russian biologists in their development, *Probl. Evol.*, 2003, vol. 5, pp. 31–39.

Kryukov, A.P. and Blinov, V.N., Interaction of hooded and carrion crows (*Corvus cornix* L. and *C. corone* L.) in the sympatry and hybridization zone: is there selection against hybrids?, *Zh. Obshch. Biol.*, 1981, vol. 42, no. 1, pp. 128–135.

Kryukov, A.P., Spiridonova, L.N., Mori, S., Arkhipov, V.Yu., Redkin, Ya.A., Goroshko, O.A., Lobkov, E.G., and Haring, E., Deep phylogeographic breaks in magpie *Pica pica* across the Holarctic: concordance with bioacoustics and phenotypes, *Zool. Sci.*, 2017, vol. 34, no. 3, pp. 185–200. https://doi.org/10.2108/zs160119

Lamichhaney, S., Han, F., Webster, M.T., Andersson, L., Grant, R.B., and Grant, P.R., Rapid hybrid speciation in Darwin's finches, *Science*, 2017. https://doi.org/10.1126/science.aao4593

Lavrenchenko, L.A., Hybridogenic speciation in mammals: illusion or reality?, *Zh. Obshch. Biol.*, 2013, vol. 74, no. 4, pp. 253–267.

Lewontin, R.C. and Birch, L.C., Hybridization as a source of variation for adaptation to new environments, *Evolution*, 1966, vol. 20, no. 3, pp. 315–336.

Liebers, D., De Knijffa, P., and Helbig, A.J., The herring gull complex is not a ring species, *Proc. R. Soc. B: Biol. Sci.*, 2004, vol. 271, pp. 893–901.

Lukyanchuk, O.A., Marova, I.M., and Redkin, Ya.A., Geographical variability of morphological and acoustic signs of the north populations of the long tailed tit *Aegithalos caudatus* (Passeriformes, Aegithalidae), *Biol. Bull.* (Moscow), 2017, vol. 44, no. 9, pp. 1081–1089.

Mallet, J., Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation, *Phil. Transact. R. Soc., B: Biol. Sci.*, 2006, vol. 363, pp. 2971–2986.

Marova, I.M. and Shipilina, D.A., Hybrid zones in birds: morphological, bioacoustic, and genetic aspects, in *XIV Mezhdunar. ornitol. konf. Severnoi Evrazii (Almaty, 18– 24 avgusta 2015 g.), Doklady* (Proc. XIV International Ornithological Conference of Northern Eurasia (Almaty, August 18–24, 2015), Reports), Almaty, 2015, pp. 373–395.

Mayr, E., Systematics and the Origin of Species from the Viewpoint of a Zoologist, Columbia University Press, 1942.

Mayr, E., *Methods and Principles of Systematic Zoology*, New York: McGraw-Hill, 1953.

Mayr, E., *Animal Species and Evolution*, Cambridge, MA: Harvard Univ. Press, 1963.

Mayr, E., *Populations, Species, and Evolution,* Cambridge (Massachusetts): Harvard Univ., 1970.

Mayr, G., Avian higher-level phylogeny: well-supported clades and what we can learn from a phylogenetic analysis of 2954 morphological characters, *J. Zool. Syst. Evol. Res.*, 2008, vol. 46, no. 1, pp. 63–72.

McCarthy, E.M., *Handbook of Avian Hybrids of the World*, Oxford University Press, 2006.

*Mezhdunarodnyi kodeks zoologicheskoi nomenklatury* (The International Code of Zoological Nomenclature), 4th ed., Moscow, 2004.

Mikhailov, K.E., Typological interpretation of a "biological species" and the ways of stabilizing the near-species taxonomy of birds, *Ornitologiya*, 2003, vol. 30, pp. 9–24.

Mikhailov, K.E., Morphogenesis and ecogenesis in the evolution of birds: the lack of their identity and its consequences, in *XIV Mezhdunar. ornitol. konf. Severnoi Evrazii (Almaty, 18–24 avgusta 2015 g.), Doklady* (Proc. XIV International Ornithological Conference of Northern Eurasia (Almaty, August 18–24, 2015), Reports), Almaty, 2015, pp. 181–204.

Mikhailov, K.E., The complexity of divergence and the species structure in birds, *Tr. Menzbir. Ornitol. O-va* (Moscow), 2017, no. 3, pp. 40–67.

Mikhailov, K.E., Ecological races and the dual nature of reproductive isolation in birds: can near-species morphological and genetic taxonomy adequately display the multifaceted population divergence in neurologically complex organisms?, *Russ. Ornitol. Zh.*, 2018, vol. 27, no. 1695, pp. 5581– 5601.

Milá, B. and Irwin, D.E., A cryptic contact zone between divergent mitochondrial DNA lineages in southwestern North America supports past introgressive hybridization in the yellow-rumped warbler complex (Aves: *Dendroica coronata*), *Biol. J. Linn. Soc.*, 2011, vol. 103, no. 3, pp. 696–706.

Miller, W., Schuster, S.C., Welch, A.J., Ratan, A., Bedoya-Reina, O.C., Zhao, F., Kim, H.L., et al., Polar and brown bear genomes reveal ancient admixture and demographic foot-

BIOLOGY BULLETIN Vol. 47 No. 7 2020

prints of past climate change, *Proc. Natl. Acad. Sci. U. S. A.*, 2012, vol. 109, no. 36, pp. e2382–e2390.

Millien, V., Morphological evolution is accelerated among island mammals, *PLoS Biol.*, 2006, vol. 4, no. 10. e321. https://doi.org/10.1371/journal.pbio.0040321

Murav'ev, I.V., On the problem of biology of the group of yellow wagtails in the Penza oblast, in *Kraevedcheskie issle-dovaniya i problema ekologicheskogo obrazovaniya* (Local Historian Research and the Problem of Environmental Education), Pensa, 1996, pp. 51–52.

Murav'ev, I.V., Comparative ecology of closely related species as exemplified by the genus *Motacilla* L., *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 1997.

Murav'ev, I.V., Breeding of the group of "yellow" wagtails in the Penza oblast, in *Ekologiya i okhrana okruzhayushchei sredy* (Ecology and Environmental Protection), Ryazan, 1993, pp. 87–88.

Opaev, A.S., The main directions of divergence of cryptic species of birds (as exemplified by the *Acrocephalus arundi-naceus* complex, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 2010.

Opaev, A.S., Redkin, Ya.A., Kalinin, E.D., and Golovina, M.V., Species limits in Northern Eurasian taxa of the common stonechats, *Saxicola torquatus* complex (Aves: Passeriformes, Muscicapidae), *Vertebr. Zool.*, 2018, vol. 68, no. 3, pp. 199–211.

Pagel, M., Venditti, Ch., and Meade, A., Large punctuational contribution of speciation to evolutionary divergence at the molecular level, *Science*, 2006, vol. 314, pp. 119–121.

Panov, E.N., *Gibridizatsiya i etologicheskaya izolyatsiya u ptits* (Hybridization and Ethological Isolation in Birds), Moscow: Nauka, 1989.

Panov, E.N., The species boundary and hybridization in birds, in *Gibridizatsiya i problema vida u pozvonochnykh* (Hybridization and the Problem of Species in Vertebrates), Sb. Tr. Zool. Muz. Mosk. Gos. Univ., 1993, vol. 30, pp. 53–96.

Panov, E.N., Interspecific hybridization in birds: evolution in action, *Priroda* (Moscow, Russ. Fed.), 2001, no. 6, pp. 51–59.

Panov, E.N., *Sorokoputy (semeistvo Laniidae) mirovoi fauny. Ekologiya, povedenie, evolyutsiya* (Shrikes (Family Laniidae) of the World Fauna: Ecology, Behavior, and Evolution), Moscow: Tov. Nauchn. Izd. KMK, 2008.

Parchman, T.L., Benkman, C.W., and Britch, S.C., Patterns of genetic variation in the adaptive radiation of new world crossbills (Aves: Loxia), *Mol. Ecol.*, 2006, vol. 15, no. 7, pp. 1873–1887.

Pavlinov, I.Ya., *Vvedenie v sovremennuyu filogenetiku* (*kladogeneticheskii aspekt*) (Introduction to Modern Phylogenetics (Cladogenetic Aspect)), Moscow, 2005.

Pavlinov, I.Ya., The species problem in biology: the origins and the present, in *Kontseptsii vida u gribov: novyi vzglyad na starye problemy (Materialy VIII vserossiiskoi mikologicheskoi shkoly-konferentsii)* (Species Concepts in Fungi: A New Look at Old Problems, Proceedings of VIII All-Russia Mycological School-Conference)), Moscow: Mosk. Gos. Univ., 2017, pp. 5–19.

BIOLOGY BULLETIN Vol. 47 No. 7 2020

Pavlinov, I.Ya., *Osnovaniya biologicheskoi sistematiki: istoriya i teoriya* (Fundamentals of Biological Taxonomy: History and Theory), Moscow: Tov. Nauchn. Izd. KMK, 2018.

Pavlinov, I.Ya., Zveri Rossii: spravochnik-opredelitel' (Animals of Russia: A Reference Guide), in 2 vols., Opredeliteli po flore i faune Rossii (Identification Guide to Flora and Fauna of Russia), Moscow: Tov. Nauchn. Izd. KMK, 2019, issue 14.

Pavlinov, I.Ya. and Lyubarskii, G.Yu., *Biologicheskaya sistematika: evolyutsiya idei* (Biological Taxonomy: The Evolution of the Idea), Moscow, 2011.

Pfander, P.V., The tragedy of the near-species taxonomy, *Russ. Ornitol. Zh.*, 2018, vol. 27, no. 1558, pp. 301–335.

Piertney, S.W., Summers, R.W., and Marquiss, M., Microsatellite and mitochondrial DNA homogeneity among phenotypically diverse crossbill taxa in the UK, *Proc. R. Soc. B: Biol. Sci.*, 2001, vol. 268, pp. 1511–1517.

Politov, D.V. and Mudrik, E.A., Molecular genetic approaches to the analysis of intraspecific structure, microtaxonomy, and microevolution in birds, *Zool. Issled.*, Moscow, 2018, no. 20, pp. 115–118.

Portenko, L.A., *Ptitsy SSSR* (Birds of the USSR), Moscow: Akad. Nauk SSSR, 1960, part 4.

Portenko, L.A., Geographic variation of rufous-throated thrush (Turdus ruficollis Pallas) and its taxonomic assessment, in *Filogeniya i sistematika ptits* (Phylogeny and Taxonomy of Birds), Tr. Zool. Inst. Akad. Nauk SSSR, 1981, vol. 102, pp. 72–109.

Potokina, E.K., Lebedeva, M.V., Ul'yanich, P.S., Levkoev, E.A., Volkov, V.A., and Zhigunov, A.V., Heteroplasmy and nuclear copies of mitochondrial genes (NUMTs) in the zone of introgressive hybridization of European spruce and Siberian spruce, in *Genetika populyatsii: progress i perspektivy* (Genetics of Populations: Progress and Prospects), Moscow, 2017, pp. 223–225.

Price, T.D., *Speciation in Birds*, Greenwood Village, CO, 2008.

Rasmussen, P.C. and Anderton, J.C., *Birds of South Asia*. *The Ripley Guide*, Washington D.C. and Barcelona: Smitsonian Institution and Lynx Edicions, 2005, vols. 1–2.

Redkin, Ya.A., New concepts of the taxonomic structure of the "yellow wagtails" group, in *Dostizheniya i problemy ornitologii Severnoi Evrazii na rubezhe vekov* (Advances and Problems of Ornithology of Northern Eurasia at the Turn of the Century), Kazan, 2001, pp. 150–165.

Redkin, Ya.A., Taxonomic relationships of forms in evolutionarily young bird complexes on the example of the genus *Motacilla* L., 1785 (taxonomic revision of the subgenus *Budytes*), *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow, 2001a.

Redkin, Ya.A., *Semeistvo Tryasoguzkovye. Polnyi opredelitel' ptits evropeiskoi chasti Rossii* (Family Motacillidae. Complete Identification Guide to Birds of European Russia), Moscow: Fiton XXI, 2012, part 3.

Redkin, Ya.A., Why it is necessary to continue purposefully collecting collection carcasses of birds on the territory of Russia and adjacent regions in the 21st century?, in *IX Mezhdunar. konf. khranitelei ornitol. koll. "Ornitologicheskie kollektsii: iz proshlogo v budushchee," Tezisy dokladov* (IX

International Conference of Ornithological Collection Keepers "Ornithological Collection: From the Past to the Future" (Moscow, October 12–16, 2015), Abstracts of Papers), Moscow, 2015, pp. 80–81.

Redkin, Ya.A. and Konovalova, M.V., On the problem of reproductive relations between two forms of yellow-browed warbler *Phylloscopus inornatus* (Blyth, 1842) based on the analysis of external morphological traits and features of distribution, *Russ. Ornitol. Zh.*, 2003, vol. 12, no. 247, pp. 1407–1430.

Red'kin, Ya.A. and Konovalova, M.V., On the taxonomy of yellow-browed warbler Phylloscopus inornatus sensu lato, based on the analysis of collection specimens (Aves: Sylvii-dae), *Zoosyst. Rossica*, 2004, vol. 13, no. 1, pp. 137–150.

Red'kin, Ya.A. and Konovalova, M.V., The eastern Asiatic races of *Sitta europaea* Linnaeus, 1758, in *Systematic Notes on Asian Birds*, no. *63, Zoologische Mededelingen Leiden*, 2006, vol. 80, no. 15, pp. 241–261.

Redkin, Ya.A., Arkhipov, V.Yu., Volkov, S.V., Mosalov, A.A., and Koblik, E.A., Species or not species? Controversial taxonomic interpretations of birds of Northern Eurasia, in *XIV Mezhdunarodnaya ornitologicheskaya konferentsiya Severnoi Evrazii (Almaty, 18–24 avgusta 2015 g.) Doklady* (Proceedings of XIV International Ornithological Conference of Northern Eurasia (Almaty, August 18–24, 2015)), Almaty, 2015, vol. 2, pp. 104–138.

Redkin, Ya.A., Arkhipov, V.Yu., Volkov, S.V., Mosalov, A.A., and Koblik, E.A., Art oder keine Art? Strittige taxonomishe Ansichten zu den Vögeln Nord-Eurasiens, *Ornithologische Mittelungen*, 2016, vol. 68, nos. 11/12, pp. 327–354.

Rubtsov, A.S., Reproductive isolation and the concept of species in birds, *Zool. Zh.*, 2015, vol. 94, no. 7, pp. 816–831.

Ryabitsev, V.K., *Ptitsy Sibiri: spravochnik opredelitel'* (Birds of Siberia: A Handbook and Identification Guide), Moscow: Yekaterinburg, 2014.

Sangster, G., Increasing numbers of bird species result from taxonomic progress, not raxonomic inflation, *Proc. R. Soc. B: Biol. Sci*, 2009, vol. 276, pp. 3185–3191.

Sangster, G., The application of species criteria in avian taxonomy and its implications for the debate over species concepts, *Biol. Rev.*, 2014, vol. 89, no. 1, pp. 199–214.

Sangster G., Integrative taxonomy of birds: the nature and delimitation of species, in *Bird Species. How They Arise, Modify and Vanish*, Switzerland AG: Springer Nature, 2018, pp. 9–37.

Song, H., Buhay, J.E., Whiting, M.F., and Crandall, K.A., Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified, *Proc. Natl. Acad. Sci. U. S. A.*, 2008, vol. 105, pp. 13486–13491.

Sotnikov, V.N., *Ptitsy Kirovskoi oblasti i sopredel'nykh territorii* (Birds of the Kirov Oblast and Adjacent Territories), vol. 2: *Vorob'inoobraznye* (Passerines), Kirov, 2006.

Soubrier, J., Gower, G., Chen, K., et al., Early cave art and ancient DNA record the origin of European bison, *Nat. Commun.*, 2016, vol. 7, pp. 1–6.

https://doi.org/10.1038/ncomms13158

Spiridonova, L.N. and Valchuk, O.P., A new case of recombination between the nuclear and mitochondrial genomes

in the genus *Calliope*: a hypothesis of the origin of *Calliope pectoralis*, in *Genetika populyatsii: progress i perspektivy* (Genetics of Populations: Advances and Prospects), Moscow, 2017, pp. 274–275.

Spiridonova, L.N., Redkin, Ya.A., Valchuk, O.P., and Kryukov, A.P., Nuclear mtDNA pseudogenes as a source of new variants of the mtDNA cytochrome *b* haplotypes: a case study of Siberian rubythroat *Luscinia calliope* (Muscicapidae, Aves), *Russ. J. Genet.*, 2016, vol. 52, no. 9, pp. 952–968.

Spiridonova, L.N., Valchuk, O.P., Redkin, Ya.A., Saito, T., and Kryukov, A.P., Phylogeography and demographic history of Siberian rubythroat *Luscinia calliope, Russ. J. Genet.*, 2017, vol. 53, no. 8, pp. 885–902.

Spiridonova, L.N., Valchuk, O.P., and Redkin, Ya.A., A new case of recombination between nuclear and mitochondrial genomes in the genus *Calliope* Gould, 1836 (Muscicapidae, Aves): the Hypothesis of Origin of *Calliope pectoralis* Gould, 1837, *Russ. J. Genet.*, 2019, vol. 55, no. 1, pp. 89–99.

Stepanyan, L.S., *Sostav i raspredelenie ptits fauny SSSR. Vorob'inoobraznye Passeriformes* (The Composition and Distribution of Birds of the Fauna of the USSR. Passeriformes), Moscow: Nauka, 1978.

Stepanyan, L.S., *Nadvidy i vidy-dvoiniki v avifaune SSSR* (Superspecies and Sibling Species in the Avifauna of the USSR), Moscow: Nauka, 1983.

Stepanyan, L.S., *Konspekt ornitologicheskoi fauny Rossii i sopredel'nykh territorii (v granitsakh SSSR kak istoricheskoi oblasti)* (Synopsis of the Avifauna of Russia and Adjacent Territories (Within the Boundaries of the USSR as a Historical Area)), Moscow: Nauka, 2003.

Summers, R.W., Jardine, D.C., Marquiss, M., and Rae, R., The distribution and habitats of crossbills *Loxia* spp. in Britain, with special reference to the Scottish crossbill *Loxia scotica*, *Ibis*, 2002, vol. 144, pp. 393–410.

Summers, R.W., Dawson, R.J., and Phillips, R.E., Assortative mating and patterns of in-heritance indicate that the three crossbill taxa in Scotland are species, *J. Avian Biol.*, 2007, vol. 38, pp. 153–162.

Taikova, S.Yu. and Redkin, Ya.A., On the forms of the group of gray shrikes in the European part of Russia and Ukraine in the light of modern ideas about the taxonomy of the complex, in *Redkie vidy ptits Nechernozemnogo tsentra Rossii. Materialy V soveshchaniya "Rasprostranenie i ekologiya redkikh vidov ptits Nechernozemnogo tsentra Rossii" (Moskva, 6–7 dekabrya 2014 g.)* (Rare Species of Birds of the Nonchernozem Center of Russia: Proceedings of the V Conference "Distribution and Ecology of Rare Species of Birds of the Nonchernozem Center of Russia" (Moscow, December 6–7, 2014)), Moscow, 2014, pp. 223–240.

*The Howard and Moore Complete Checklist of the Birds of the World*, Dickinson, E.C. and Remsen, J.V., Eds., 4th ed., Eastbourne, 2013, vol. 1.

*The Howard and Moore Complete Checklist of the Birds of the World*, Dickinson, E.C. and Christidis, L., Eds., 4th ed., Eastbourne, 2014, vol. 2.

Thomson, S.A., Pyle, R.L., Ahyong, S.T., Alonso-Zarazaga, M., Ammirati, J., Araya, J.F., et al., Taxonomy based on science is necessary for global conservation, *PLoS Biol.*, 2018, vol. 16, no. 3. e2005075.

https://doi.org/10.1371/journal.pbio.2005075

Tobias, J.A., Seldon, N., Spottiswoode, C.N., Pilgrim, J.D., Fishpool, L.D.C., and Collar, N.J., Quantitative criteria for species delimitation, *Ibis*, 2010, vol. 152, no. 4, pp. 724–746.

Töpfer, T., Haring, E., Birkhead, T.R., Lopes, R.J., Severinghaus, L.L., Martens, J., and Päckert, M., A molecular phylogeny of bullfinches *Pyrrhula brisson*, 1760 (Aves: Fringillidae), *Mol. Phylogenet. Evol.*, 2011, vol. 58, pp. 271–282.

Valchuk, O.P., Redkin, Ya.A., and Sotnikov, V.N., The first record of the red-throated thrush *Turdus ruficollis* and new finds of birds with phenotypes of the group of dark-throated thrushes *T. ruficollis* and *T. atrogularis* in Primorye, *Russ. Ornitol. Zh.*, 2013, vol. 22, no. 947, pp. 3315–3320.

Vasil'eva, L.N., The hierarchy and combinatorics of traits in evolutionary taxonomy, *Tr. Zool. Inst. Ross. Akad. Nauk*, 2009, suppl. 1, pp. 235–249.

Vaurie, Ch., The Birds of the Palearctic Fauna. Order Passeriformes, London, 1959.

Vijay, N., Bossu, Ch.M., Poelstra, J.W., Weissensteiner, M.H., Suh, A., Kryukov, A.P., and Wolf, J.B.W., Evolution of heterogeneous genome differentiation across multiple contact zones in a crow species complex, *Nat. Commun.*, 2016, vol. 7, pp. 1–10.

https://doi.org/10.1038/ncomms13195

Vinarskii, M.V., The fate of the subspecies category in zoological taxonomy. 1. History, *Zh. Obshch. Biol.*, 2015a, vol. 76, no. 1, pp. 3–14. Vinarskii, M.V., The fate of the subspecies category in zoological taxonomy. 2. Modernity, *Zh. Obshch. Biol.*, 2015b, vol. 76, no. 2, pp. 99–110.

Wiley, E.O. and Liberman, B.S., *Phylogenetics: The Theory* and *Practice of Phylogenetic Systematics*, Hoboken, 2011.

Wiley, E.O. and Mayden, R.L., Species and speciation in phylogenetic systematics, with examples from the North American fish fauna, *Ann. Missouri Bot. Garden*, 1985, vol. 72, pp. 596–635.

Zablotskaya, M.M., Voice responses of eastern and European goldfinches (Passeres, Carduelinae): form and functional significance of calls, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1975, vol. 80, no. 3, pp. 22–38.

Zelenkov, N.V., Methods of phylogenetics and evolutionary biology: advances and limitations, in *XIV Mezhdunar. ornitol. konf. Sev. Evrazii (Almaty, 18–24 avgusta 2015 g.). Doklady* (XIV International ornithological conference of Northern Eurasia (Almaty, August 18–24, 2015), Reports), Almaty, 2015, vol. 2, pp. 138–165.

Zhang, Z-Q., Animal biodiversity: an update of classification and diversity in 2013, *Zootaxa*, 2013, vol. 3703, no. 1, pp. 5–11.

https://doi.org/10.11646/zootaxa.3703.1.3

Zink, R.M., The role of subspecies in obscuring avian biological diversity and misleading conservation policy, *Proc. R. Soc. B: Biol. Sci.*, 2004, vol. 271, pp. 561–564.

Translated by N. Smolina