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**ANIMAL GENETICS**

# A Karyological Study of Some Corvine Birds (Corvidae, Aves)

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**Abstract**—Karyotypes were studied in the hooded and carrion crows, their naturally occurred hybrids, the jungle crow, the azure-winged magpie ($2n = 80$ in all aforementioned birds), and the magpie ($2n = 82$). Corvine birds of Primorskii Krai were karyotyped for the first time. In addition to the similarity in the diploid chromosome sets, corvine birds were shown to have a similar structure of karyotype: in all studied birds, 14 macrochromosomes (Mchs) classified into three groups according to their size were detected. By karyotype structure, birds belonging to the same genus are similar. Some intergeneric differences are due to a change in the position of centromeres of the largest and sex chromosomes. Karyotypes of interspecific hybrids of crows are remarkable for the presence of heteromorphic (t/st) chromosome pair 2 in some individuals, which apparently does not affect their fecundity. Using differential C-banding, the sex chromosome W in female magpies was identified. In addition, heteromorphism was detected in C-bands of homologs of Mch pair 4 in the hooded crow. In the jungle crow, the azure-winged magpie, and the magpie, bright QH-bands and numerous G-bands were detected on Mchs and on some microchromosomes only. Active Ag-NOR-bands were detected on one macrochromosome pair in the magpie. In all, the karyotype structure of corvine birds is comparable to the basic structural scheme of the karyotype in the order Passeriformes, which confirms the concept of conservatism of the avian karyotype.

## INTRODUCTION

Avian karyology still remains poorly studied (as compared, for example, to mammalian karyology). Of more than 9000 bird species of the modern world ornithofauna, about 400 species (less than 5%) have been cytogenetically studied [1]. The fact that avian chromosomes have been poorly studied is partly related to difficulties in collection of the material but is mainly associated with the specific structure of avian karyotype. This karyotype is characterized by conservatism. For example, many birds belonging to various families of Passeriformes have a typical or basic karyotype of similar chromosome size and diploid numbers close to the modal value (i.e., $2n = 80$) [1–4]. Another specific characteristics of avian karyotype is high diploid numbers and conventional division of chromosomes into two groups: (1) a small group of large chromosomes or macrochromosomes (**Mchs**) and (2) a very large group of small chromosomes (which frequently cannot be morphologically identified) or microchromosomes (**mchs**). Therefore, detailed analysis of the total karyotype is impossible, and usually (even using routine staining techniques) only macrochromosomes are analyzed. In contrast to mammalian karyology, modern cytogenetic methods (differential staining) are rarely used in avian karyology.

The family Corvidae includes more than 100 species which are widely spread throughout the world [5]. Of these, only 14 species have been karyologically described [6–20]. Most descriptions are given at the level of β-karyology.

This work is devoted to an intergeneric and interspecific comparative study of karyotype of corvine birds. Particular attention is given to a comparison of closely related species of crows: the hooded crow *Corvus cornix cornix* Linnaeus, 1758; the carrion crow *Corvus corone orientalis* Eversmann, 1841; and phenotypically different hybrids *C. cornix cornix* × *C. corone orientalis* from the Siberian hybridization zone. These hybrids are of particular interest in the studies of hybrid genome and possible abnormalities in hybrid karyotypes. We also analyzed the karyotypes of yet unstudied subspecies of some species belonging to the ornithofauna of Primorskii Krai: the jungle crow *Corvus macrorhynchos mandshuricus* Buturlin, 1913; the azure-winged magpie *Cyanopica cyanus cyanus* Pallas, 1776; and the magpie *Pica pica jankowskii* Stegmann, 1928.

## MATERIALS AND METHODS

Chromosome preparations of 28 corvine birds (seven hooded crows, six carrion crows, nine hybrids between these two species, one jungle crow, two azure-winged magpies, and three magpies) served as material for this study (Table 1). The taxonomy of the studied corvine birds is given according to Stepanyan [21]. Birds were captured during field work in 1990–1999. Chromosome preparations were made from bone mar-

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**Table 1.** Number, sex, and sampling locality of corvine birds

| Species | ♂♂ | ♀♀ | Sampling locality |
|---|---|---|---|
| *Corvus cornix cornix* | 2 | – | Tisul', Kemerovo oblast |
| | 3 | 2 | Vicinity of Novosibirsk city |
| *C. corone orientalis* | 3 | 1 | Cherga, Altai Mountains |
| | – | 1 | Tisul', Kemerovo oblast |
| | 1 | – | Novonezhino, Primorskii krai |
| *C. c. cornix* × *C. c. orientalis* | 4 | 5 | Tisul', Kemerovo oblast |
| *C. macrorhynchos mandshuricus* | 1 | – | Vladivostok city, Primorskii krai |
| *Pica pica jankowskii* | 1 | 2 | Nadezhdinskoe, Primorskii krai |
| *Cyanopica cyanus cyanus* | 2 | – | Konstantinovka, Primorskii krai |

row of chicks by two methods: (1) a standard direct technique [22] and (2) the method of short-term cell culturing [23, 24] with slight modifications (DMEM and RPMI-1640 were used as intermediate media). It was noted that the quality of squash chromosome preparations is better on preparations obtained using culture media. Some preparations were obtained using the yeast stimulation suggested for mammalian chromosomes [25]. Sex of chicks was determined by chromosomal analysis: the sex-chromosome sets ZZ and ZW were found in respectively males and females, which in birds are heterogametic.

Preparations were stained using a standard technique with a 2% Giemsa solution in a phosphate buffer, pH 6.8. Some preparations were differentially stained: C-banding [26], G-banding [27, 28] with modifications, QH-banding [29], Ag-NOR-banding [30]. Designations of chromosome morphology are given according to the classification of Levan *et al.* [31]: t, acrocentric (= telocentric), st, subtelocentric; sm, submetacentric; and m, metacentric.

Chromosome preparations were examined using Biolar and Jenaval microscopes at a magnification of 1000×. A Mikrat-Izopan film was used for microphotographs.

## RESULTS

### *Standard Staining*

*The genus Corvus.* A comparison of karyotypes of birds belonging to the genus *Corvus* (the carrion crow, the hooded crow, their hybrids, and the jungle crow) revealed that they are very similar. In each species, a diploid set includes 80 chromosomes that form a decreasing series. Of these, we classified the largest 14 chromosomes (in females, 13 chromosomes) as Mchs (Figs. 1, 2a). They can conventionally be split by their size into three groups. The first group includes the largest pair of Mchs (pair 1), which is distinguished from the other pairs of Mchs not only by size, but also by morphology. It is submetacentric, whereas the other pairs of Mchs are subtelocentric. The second group is represented by two pairs of Mchs of smaller size. The third group includes four Mch pairs: pairs 4, 5, 6 (having approximately equal size), and 7 (having a slightly smaller size). This group also includes the sex chromosomes Z. It is often difficult to determine the precise position of the sex chromosomes because of similarity of chromosomes of the third group by both size and morphology. In our opinion, the subtelocentric Z chromosome should be placed at position 6 in the decreasing series in the carrion, hooded, and hybrid crows. In the jungle crow, we did not identify sex chromosomes, because we studied only one male. The sex chromosome W of females occupies an intermediate position between Mchs and mchs of the chromosome set, i.e., position 8 (Fig. 1). In some cases of metaphase plates with low spiralization, one can also determine the morphology of mch pair 8 to 10, which are subtelo- or submetacentric. Besides, two metacentric mch pairs are detectable, which approximately occupy positions 12 and 13 in the descending series.

In two males of hybrid crows, we detected heteromorphism of homologs of Mch pair 2: one homolog is subtelocentric and the other, acrocentric (Fig. 1c). These crows are likely to be mosaics: the percentage of cells with heteromorphic (st/t) Mch pair 2 is 27.5 in one and 22.5% in the other of them. Unfortunately, we could not assess meiosis defects in these crows, because we studied chicks rather than adult birds. To elucidate the nature of this variation in Mch pair 2, further studies are needed (C- and G-banding on chromosomes of hybrids and the investigation of meiosis in hybrids).

*The genus Cyanopica.* In two studied male azure-winged magpies, the karyotype consists of 80 chromosomes, of which 14 are Mchs. The latter are split into three groups, as in crows. The first group includes the largest pair of submetacentric Mchs, the second group consists of two pairs of subtelocentric Mchs, and the third group is represented by four pairs of subtelocentric Mchs, including two Z sex chromosomes. As we studied males, we can only state about the position of sex chromosomes in the decreasing series that they belong to the third size group. We do not present the karyotype of an azure-winged magpie from Primorye, because we did not find any differences with the kary-


**Fig. 1.** Karyotype of (a) a female carrion crow *C. corone orientalis* (Altai Mountains, 2*n* = 80), (b) a female hooded crow *C. cornix cornix* (Novosibirsk, 2*n* = 80), and (c) a hybrid male *C. corone* × *C. cornix* (Kemerovo oblast, 2*n* = 80). In the hybrid, Mch pair 2 with different morphology of t/st homologs is boxed and sex chromosomes Z and W are shown separately.

otype described in the same subspecies from Siberia and another subspecies from China [10, 16, 19].

*The genus Pica.* The studied magpies of genus *Pica* had a karyotype consisting of 82 chromosomes which form a series sharply decreasing by size (see Fig. 2b). Fourteen (in females, 13) largest chromosomes are classified as Mchs, the remaining are mchs. In the magpie, Mchs are also split into three groups. All macroautosomes except submetacentric Mch pair 1 are subtelocentric. Similar to the karyotypes of crows, the first group includes the largest Mch pair 1. Mch pairs 2 and

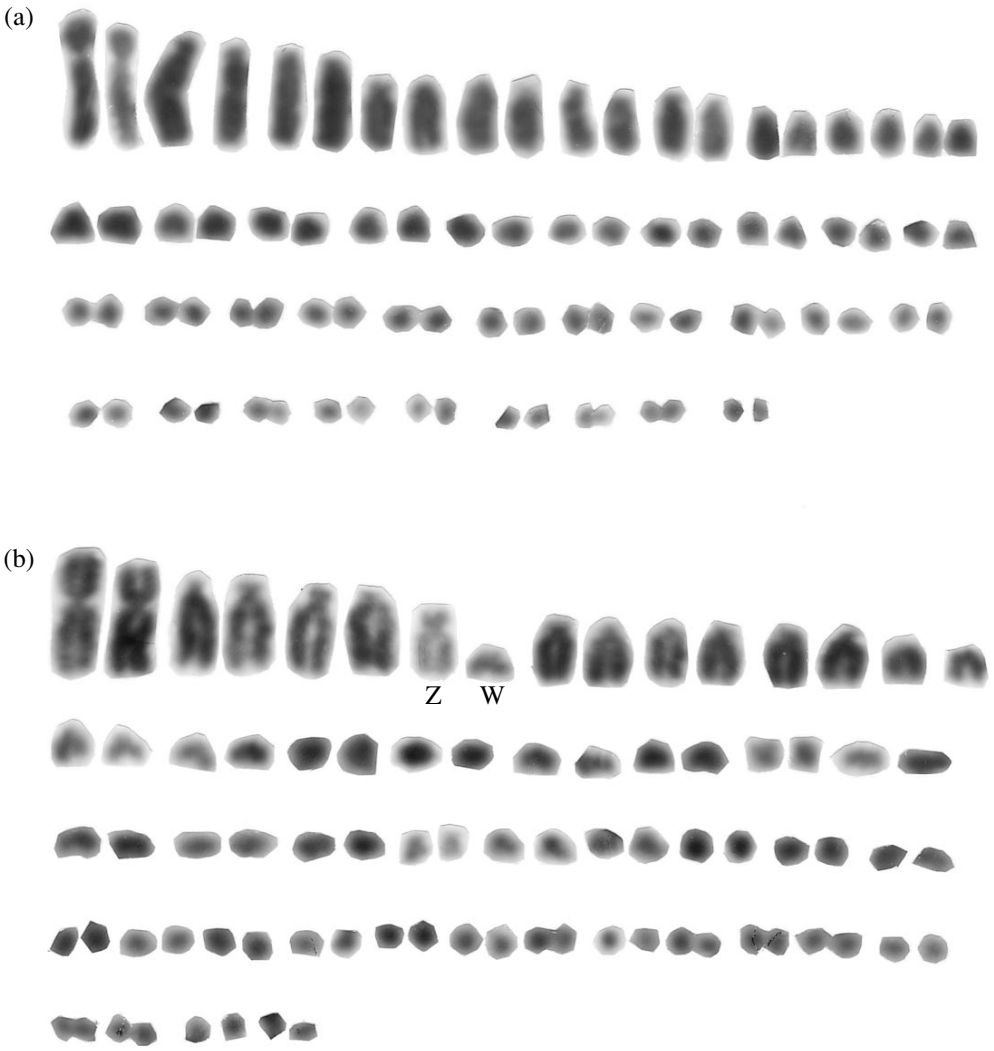


**Fig. 2.** Karyotype of (a) a male jungle crow *C. macrorhynchos mandshuricus* (Primorskii Krai, 2*n* = 80) and (b) a female magpie *P. pica jankowskii* (Primorskii Krai, 2*n* = 82).

3 are smaller and similar in size; they are included in the second group. The third group includes Mch pairs 4, 5, 6, and 7, which are similar in size. The position of the Z chromosome is well identifiable. As the Z chromosome of *Corvus* and *Cyanopica*, it occupies position 4 and is assigned to the third size group, but in the genus *Pica* this chromosome is submetacentric, whereas in *Corvus* and *Cyanopica* it is subtelocentric. The W chromosome of females is metacentric, occupies position 11 in the decreasing series, and is classified with mchs. The transition from Mchs to mchs is sharper in magpies than in crows, though on good metaphase plates it is also possible to identify mch pairs 8 to 10 by their morphology. It is likely that only one metacentric pair is found among the smaller mchs of the magpie.

### *Differential Staining*

Avian chromosomes were found to have a lower capability of differential banding, as compared, e.g., to mammalian chromosomes.

*C-banding.* In the carrion, hooded, and jungle crows, the azure-winged magpie, and the magpie of genus *Pica*, C-banding revealed the presence of slight C-bands in pericentromeric regions of Mchs. Some of small mchs was almost completely C-positive (Figs. 3a, 3b). In addition, we found a relatively bright C-band in the pericentromeric region of one of homologs of Mch pair 4 in the hooded crow (this band almost totally covers the short arm), whereas the pericentromeric C-band of the other homolog is dull and has a smaller size (Fig. 3a). Thanks to C-banding, we identified the W chromosome in female magpies of genus *Pica*. This chromosome appeared to consist almost totally of C-heterochromatin (Fig. 3b).

*G-banding.* In the jungle crow, the magpie, and the azure-winged magpie, G-banding revealed a complex pattern of bands throughout the entire length of all Mchs and some of mchs (approximately, up to pair 17), including the W sex chromosome of female magpies of genus *Pica* (Figs. 3c–3e). Some mchs were found to be

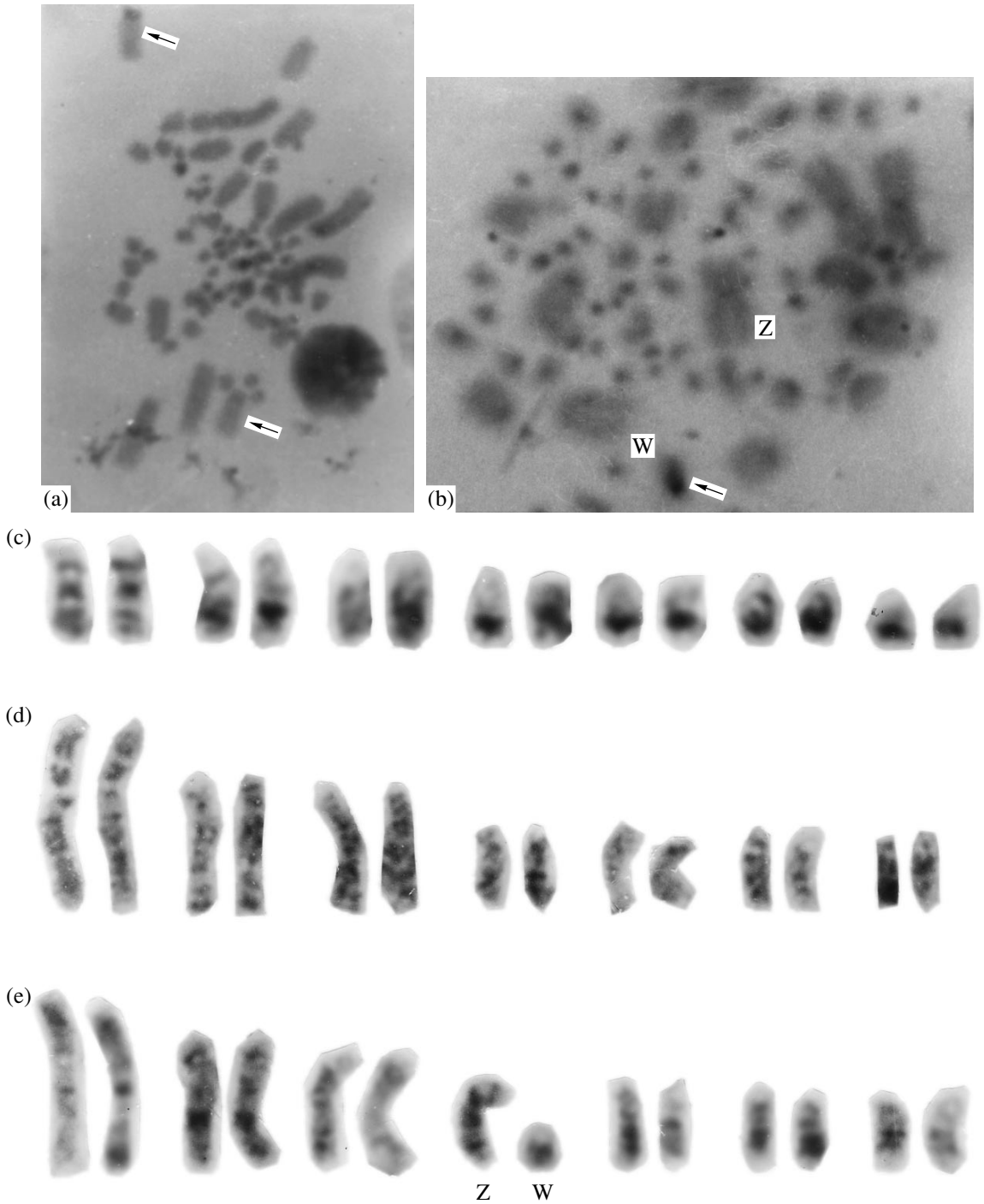


**Fig. 3.** C-banding: (a) a male carrion crow (Mch pair 4 is indicated by arrows. One of homologs has a bright telomeric C-band and the other has a dull telomeric C-band.); (b) a female magpie (The arrow indicates the sex chromosome W which totally consists of C-heterochromatin. One can see slight pericentromeric bands of Mchs and some mchs). G-banding on Mchs of (c) a male jungle crow, (d) a male azure-winged magpie *Cyanopica cyanus cyanus*, and (e) a female magpie.

G-positive and have bright G-bands, mostly near telomeric chromosome regions. Pericentromeric chromosome regions are G-negative. Most mchs are G-negative.

*Ag-NOR-banding.* We studied this type of banding in the jungle crow and the magpie of genus *Pica*. In the magpie, we could identify an active nucleolus-organizing region (NOR) on a mch pair which occupies an approximate position of 16 to 18 in the decreasing series (Fig. 4a).

*QH-banding* (using two fluorochromes, quinacrine and Hoechst 33258) is specified for the detection of AT-

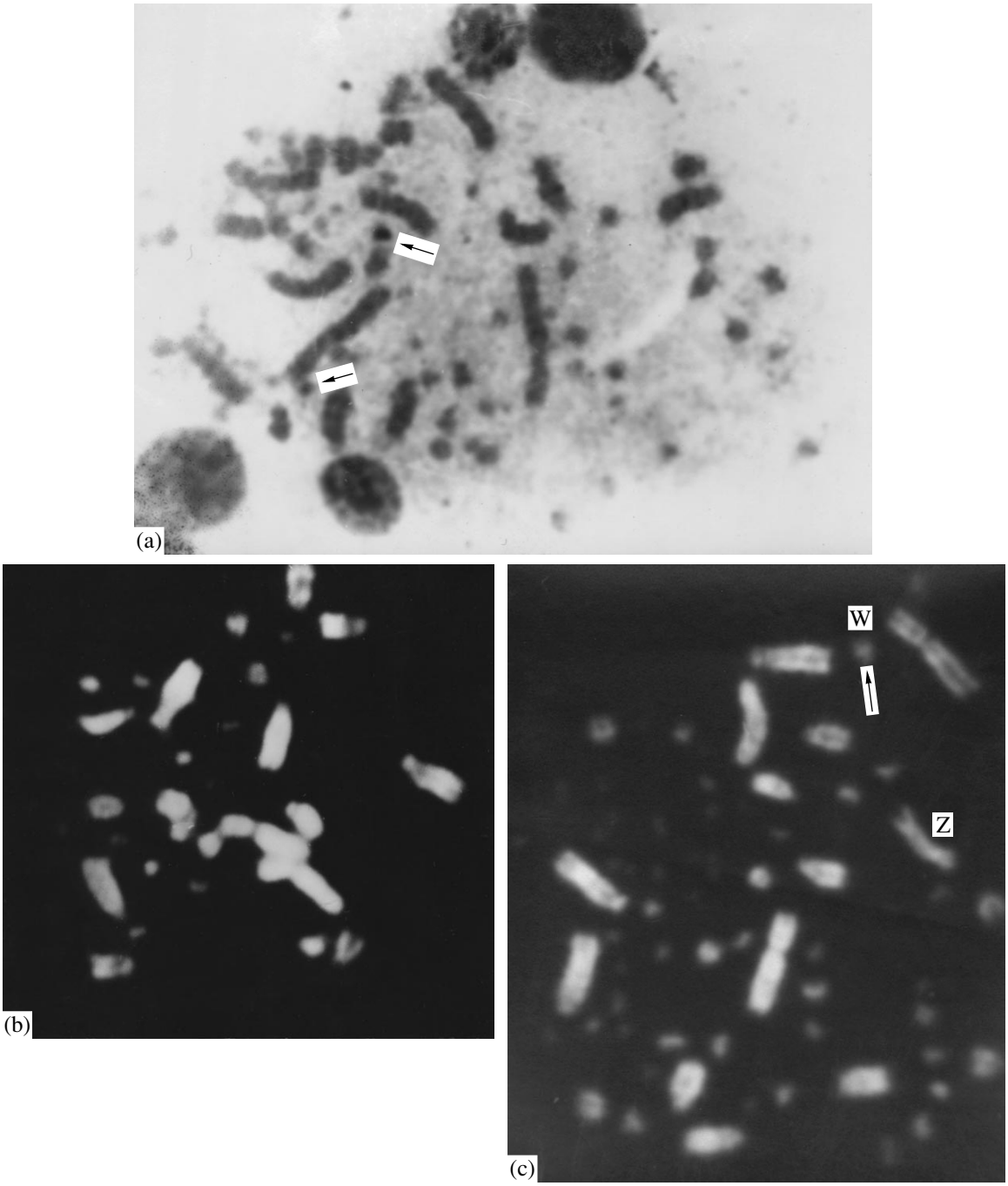


**Fig. 4.** (a) Ag-NOR-banding in a magpie. A pair of mchs with active NORs is indicated by arrows. QH-banding on chromosomes of (b) a male azure-winged magpie and (c) a female magpie. The arrow indicates the sex chromosome W with a dull fluorescence.

rich regions of chromosomal DNA, which have a bright fluorescence. We studied QH-banding on chromosomes of the jungle crow, the magpie, and the azure-winged magpie (Figs. 4b, 4c). We found that Mchs and only some mch have bright fluorescent regions along their length. QH-negative bands correlated with pericentrometic regions of chromosomes; i.e., the similarity between G- and QH-negative bands is evident. Approximately one-third of mchs was QH-negative, and the sex chromosome W of female magpies had a dull fluorescence (see Fig. 4c). Probably, this indicates that AT-rich DNA is related to the regions of bright fluorescence and the W chromosomes of the magpie and some mchs contain other (GC-rich) DNA. As a rule, Q-bands with bright fluorescence correspond to dark G-bands.

## DISCUSSION

It is known from the literature that diploid numbers in different species of genus *Corvus* vary from 72 to 80;

**Table 2.** Distribution of diploid chromosome sets and the position and constitution of sex chromosomes in the karyotypes of corvine birds

| Family Corvidae | 2*n* | Number of Mchs* | Z chromosome | W chromosome | Source |
|---|---|---|---|---|---|
| *Dendrocitta vagabunda* | 80± | (13)** | 4 t | 7 t | [15] |
| *D.v. vagabunda* | 74± | 16 | 3 st | 5 st | [13] |
| *Garrulus glandarius* | 78± | (13) | 4 sm | 6 t | [19] |
| *Pyrrhocorax pyrrhocorax* | 80± | 14 | 4 m | – | [19] |
| | 76 | 14 | n.d. | | [10, 16] |
| *Cyanocitta cristata* | 78± | 22 | 4 sm | 10 sm | [8, 12] |
| *Cyanopica cyanea* | 80± | 14 | 4 st | 8 t | [16] |
| *C. cyana* | 80 | 14 | 4 st | t | [19] |
| *C. cyanus cyanus* | 80 | 14 | st | – | Our data |
| *Pica pica* | 76 | 22 | 4 sm | 11 m | [7] |
| | 76± | n.d. | n.d. | n.d. | [20] |
| | 76 | 22 | 4 sm | 11 m | [12] |
| | 82 | n.d. | n.d. | n.d. | [6] |
| *P.p. jankowskii* | 82± | 14 | 4 sm | 11 sm–m | Our data |
| *Corvus frugilegus* | 80 | n.d. | n.d. | n.d. | [20] |
| *C. brachyrhynchos* | 80± | 22 | 4 st | 9 st | [8, 12] |
| *C. corax* | 78 | 14 | 6 st | 8 sm–st | [11] |
| *C. monedula monedula* | 80 | 14 | 4 sm | t | [9, 10, 16] |
| *C. splendens* | 78± | 14 | 6 st | 8 st | [15] |
| *C. s. splendens* | 80± | 14 | 4 st | 8 t | [14] |
| *C. macrorhynchos* | 78± | 14 | 6 st–t | 8 st | [15] |
| *C. m. culminatus* | 80± | 14 | st | – | [14] |
| *C. m. mandshuricus* | 80± | 14 | 6 st | – | Our data |
| *C. corone corone* | 72 | (13) | 4–5 st | 8 sm | [18] |
| *C. c. orientalis* | 80 | n.d. | n.d. | n.d. | [20] |
| *C. c. orientalis* | 80± | 14 | 6 st | 8 st | Our data |
| *C. c. cornix* | 80 | 14 | 4 m | – | [17] |
| *C. cornix* | 80 | n.d. | n.d. | n.d. | [20] |
| *C. c. cornix* | 80± | 14 | 6 st | 8 st | Our data |
| *C. corone orientalis* × *C. cornix cornix* | 80 | n.d. | n.d. | n.d. | [20] |
| | 80± | 14 | 6 st | 8 st–sm | Our data |

Note: The nomenclature and chromosomal characteristics are given according to cited works. The data from works on the karyology of corvine birds, which were published before 1959, are not presented because of imperfect techniques. Designations: n.d., no data available, i.e., the author only indicates the diploid number, and any other detailed data are not available.

* The number of Mchs, including the sex Mchs.

** In parentheses, the number of Mchs is given for females, if only females were studied.

2*n* = 80 in corvine birds of genus *Cyanopica*; in birds of genus *Pica* (the magpie from Europe was described), 2*n* = 76 or 82, according to the data of different authors (Table 2). Based on our data, corvine birds of genera *Corvus* and *Cyanopica* have 2*n* = 80, and birds of genus *Pica* have 2*n* = 82. Our study revealed that the studied corvine birds are similar in both the diploid numbers and the size structure of karyotype, which is reflected in classification of 14 Mchs into three size groups. The similarity in the structure of chromosome sets also applies to other species of genus *Corvus*, as well as to the studied members of genera *Garrulus*, *Pyrrhocorax*, and *Cyanocitta* (see Table 2). Judging from the karyotype of *Dendrocitta vagabunda* described by some authors [13, 15], this species, though it has diploid numbers close to corvine birds (according to [13, 15], 74 and 80, respectively), stands apart from other corvine birds by size structure of its karyotype, because the

Z chromosome is related to the second size group in this species, whereas this chromosome is assigned to the third size group in other karyotyped Corvidae. Apparently, as regards the determination of exact diploid numbers, some divergence in opinion between the authors may be explained by technical errors, and various designations of chromosome morphology are related to different interpretation of morphological types of chromosomes. For instance, if the centromere is situated in close proximity to the end of the chromosome and short arms are distinguishable, some authors classify this chromosome as acrocentric (designated by t in Table 2), whereas other authors (including us) consider it subtelocentric (in Table 2, st). The degree of chromosome spiralization, which shows a curvilinear relationship with the number of microchromosomes [32], plays a significant part in the determination of the exact diploid number of chromosomes. Therefore, the authors recommend the use of metaphase plates in which the length of chromosome 1 is 10.5 to 12 μm, i.e., with low or moderate chromosome spiralization.

In addition to evident similarity between the karyotypes of corvine birds, we detected some minor karyotypic differences between genera. These differences touch upon the variation in size and in centromere position of larger Mchs and Z chromosomes. Thus, in the studied birds of genus *Corvus*, Mch pair 1 was submetacentric and looked subtelocentric on metaphase plates with higher degree of spiralization, whereas in the studied birds of genera *Cyanopica* and *Pica* the position of centromere was more submedian, although this pair of Mchs was also submetacentric in these two genera. The morphology of the Z chromosome also varied from subtelocentric in genera *Corvus* (except *C. monedula* [16] with a submetacentric Z chromosome) and *Cyanopica* to submetacentric in genera *Pica*, *Garralus*, *Cianocitta*, and *Pyrrchocorax* (our interpretation of data presented in Table 2). Only minor variation of diploid numbers was observed: $2n = 78–80$ in birds belonging to genera *Corvus*, *Cyanopica*, *Dendrocitta*, *Garralus*, and *Pyrrchocorax* and $2n = 76$ and 82 in birds of genus *Pica* (see Table 2). Therefore, we may suggest that chromosomal rearrangements belonging to the type of pericentric inversion play an important part in evolution of corvine birds. This type of chromosomal rearrangements is also characteristic of many passerine birds [2, 4, 15, etc.].

The detection of karyotypic polymorphism in hybrids is noteworthy, in view of the fact that parental species (the carrion and hooded crows) had identical karyotypes. Phylogenetically related bird species often have similar or identical karyotypes [7, 9, 15, 17], but their hybrids have reduced fecundity and may have abnormalities of meiosis, as shown in a duck hybrid *Anas clypeata* × *A. penelope* [33]. In hybrids between the carrion and hooded crow, meiosis has not been studied, but, according to the opinion of zoologists who worked in the Siberian hybridization zone, these hybrids have roughly the same fecundity as the parental forms [34, 35]. In a similar hybridization zone of the hooded and carrion crows situated in the southern Alps, hybrid females had reduced fecundity, but it was compensated by greater reproductive success of hybrid males [36]. In artificially obtained hybrids between *Falco peregrinus* and *F. mexicanus* (which have identical karyotypes), reduced fecundity of hybrid females was also observed, whereas hybrid males successfully mated with the parental forms; the fertility of hybrid progeny was not proved [37].

The cases of autosome polymorphism for various pairs of avian Mchs (frequently, for pairs 2, 3, and 5) are described in a review by Shields [4]. In the order Passeriformes, inversion polymorphism is widespread in the family Emberizidae, but the correlation of polymorphism with phenotypic traits was detected only in two cases. The first is the correlation of inversion polymorphism for Mch pair 2 with crown color and behavior in *Zonotrichia albicollis* [38]. The second is the correlation found between beak and tail sizes, plumage, and karyotype polymorphism for Mch pairs 2 and 3 in the same species or for Mch pairs 2 and 5 in *Junco hyemalis* [39]. Other authors [40], who found inversion polymorphism for Mch pairs 3 and 5 in other *Z. capensis* (Emberezidae), suggested that inversions can play a great part in the formation of abnormal chromosomes and nonviable gametes and cause a decrease in fecundity in heterozygote carriers of an inversion. As an inverted fragment can accumulate mutations, various karyotypes can be related to specific adaptive characteristics of an organism. Thus, we can suggest that the chromosome polymorphism in birds is adaptive. Note that the study of a large number of birds is necessary for the detection of polymorphism in bird taxa with similar karyotypes; however, the karyotypes of species are often described based only on one or two individuals.

Although chromosome banding techniques were found to be less informative in birds than, for example, in mammals, they are nevertheless important for avian cytogenetics. Thus, thanks to C-banding, we succeeded in the detection of the sex chromosome W in female magpies and in the determination of its position in the size series. In birds, C-banding is primarily considered a diagnostic technique for the detection of the W chromosome [28, 41, 42]. As the Y chromosome in mammals, the W chromosome is completely C-positive and often almost totally consists of heterochromatin [42–46, etc.], although it may also consist of euchromatin, as in some ratite birds (Ratitae) [47]. In birds, homologs often have different banding pattern. Thus, for example, different C-bands were found in homologs of the Z chromosome in the domestic chicken [43] and the Japanese quail [44, 48]. C-banding heteromorphism of homologs, which we found on chromosomes of pair 4 in the hooded crow, is also known for embryos of the Japanese quail [48]. In the cells of some embryos, the short arm of chromosome 4 had a much longer C-segment in one or both homologs. Apparently, the addition or loss of heterochromatin on the Z chromosomes and

other Mchs do not significantly affect vital functions in birds, because these cases are found not only in Passeriformes, but also in some nonpasserine bird species [49].

In the studied corvine birds, QH-banding (AT-specific type of banding) revealed that the W chromosome of females and a major part of mchs were QH-negative, because they are likely to contain GC-rich DNA. In addition, duller fluorescence of the W chromosome and other mchs is likely to be related to different degree of compactization of chromatin, because it is known that middle-size and small avian mchs (in contrast to Mchs) "lack the higher level of compactization of chromosomal material, i.e., their chromonema does not form complete spiral coils" [50, p. 597]. Recently, a series of works was published on chromosome banding with GC-specific fluorochromes and on gene mapping onto chromosomes of the domestic chicken and some other birds. On this type of banding, most mchs have a bright fluorescence, because it was found out that avian mchs mostly consist of GC-rich and often late-replicating DNA [50–52]. It is interesting that approximately 75% of all mapped genes of the domestic chicken were particularly assigned to mchs [50, 53], and the frequency of crossing over in them is high. This is additional evidence that mchs represent a stable and essential part of avian karyotype.

The active NORs found on mchs of the magpie is an example of gene localization on mchs. In most cases of other birds, NORs are also assigned to mchs [41, 46, 52, 54, 55], but they may also be detected on Mchs, as demonstrated by Japanese authors in three species of the order Strigiformes [56].

Earlier, extraordinary evolutionary conservatism of the avian Z chromosome (similarly to the mammalian X chromosome) was demonstrated [17, 46, 57, 58, etc.]. This conservatism is manifested as follows: most frequently, the Z chromosome of birds occupies positions 4 or 6, is meta- or submetacentric, and has identical G-banding pattern in various bird taxa. By contrast, the sex chromosome W is the most variable. In various corvine birds, it differs in morphology and position in the size series (Table 2). In birds, the differences in the morphology of the W chromosome were detected not only between different species, but also between different populations of the same species [59]. Two conserved *CHD* genes mapped onto the sex chromosomes were detected in all except ratite birds [60, 61].

The evidence for the conservative nature of avian karyotypes has been accumulating. Thus, a significant homology between nine chromosome pairs was detected by fluorescent in situ hybridization (FISH) in the domestic chicken and the emu [62]. In addition, it was demonstrated that chromosomes of birds belonging to one or several orders contain several conserved elements in DNA sequence [63, 64]. Some authors found a high degree of similarity in G-banding pattern of at least larger avian Mch pairs 1 to 3 not only between phylogenetically related species and genera, but also between representatives of different avian orders [17, 23, 43, 49, 56, 65].

Thus, we found that the structure of karyotype of Corvidae is close to the basic structure of karyotype suggested by Bulatova [66] for representatives of the entire order Passeriformes. The family Corvidae is considered one of the most ancient in the order Passeriformes [17], and, probably, the karyotype of Corvidae can be considered close to ancestral karyotype. Apparently, inversion-type chromosomal rearrangements occur in phylogeny of this family, but their fixation rate is low, which corresponds to the ideas on the low rate of chromosomal and molecular evolution in birds [67, 68].

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