Inheritance Patterns of Lateral Dimorphism Examined through Breeding Experiments in Tanganyikan Cichlid (Julidochromis transcriptus) and Japanese Medaka (Oryzias latipes)

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The asymmetry of mouth morphology, in which the mouth opens either leftward or rightward, is a unique example of antisymmetry that is widely found in fishes, such as Tanganyikan scale-eating cichlids, herbivorous cichlids, and the Japanese freshwater goby. This dimorphism is thought to be heritable in a Mendelian manner similar to that of the dominance of the lefty allele over righty, with homozygotes of lefty alleles being absent. This study aims to reveal whether this trait is inherited in the same Mendelian manner in fishes other than those examined to date, and whether the absence of the dominant homozygote is due to a lethal effect. We conducted F_1 and F_2 breeding experiments using the Tanganyikan cichlid *Julidochromis transcriptus* and Japanese medaka *Oryzias latipes*. For both *J. transcriptus* and *O. latipes*, the F_1 generations produced by incrossing lefty parents showed a lefty:righty ratio of 2:1, whereas incrosses of righties produced only righty offspring. Test crosses between lefty and righty produced a 1:1 ratio of lefty and righty offspring. These results are consistent with the inheritance model in which righty is homozygous for a recessive righty allele and lefty is heterozygous for dominant lefty and recessive righty alleles, in agreement with previous observations. The F_2 test cross also confirmed this pattern. Furthermore, no lethal effects on hatchability of *O. latipes* were detected, refuting the suggestion that the dominant homozygote is embryonic lethal. We conclude that mouth laterality is inherited in the same Mendelian manner in these two species, similar to that other fish species studied previously. However, the reason for absence of the dominant homozygote remains unclear.

Key words: fish, mouth asymmetry, laterality, Mendelian inheritance, medaka

INTRODUCTION

Morphological asymmetry of the mouth was first described in seven species of Tanganyikan scale-eating cichlids belonging to the genus *Perissodus* (Liem and Stewart, 1976; Hori, 1991, 1993). In these fishes, the mouth of one morph type (designated "lefty"; Nakajima et al., 2004) opens to the right with the left side of the head facing the front, while in the other ("righty"), the mouth opens to the left with the right side of the head facing forwards. Such morphological laterality has been reported in several other fishes, including the Tanganyikan cichlids *Telmatochromis temporalis* (Mboko et

al., 1998), *Neolamprologus moorii* (Hori et al., 2007), and *Neolamprologus fasciatus* (Takeuchi and Hori, 2008), the scale-eating tricanthodid *Macrorhamphosodes uradoi* (Nakae and Sasaki, 2001), the Japanese riverine goby *Rhinogobius flumineus* (Seki et al., 2000), and the large-mouth bass *Micropterus salmoides* (Nakajima et al., 2007; Yasugi and Hori, 2011).

This morphological laterality is closely associated with behavioral laterality. The scale-eating cichlid, *Perrisodus microlepis*, is a well-known example in which righty individuals always attack the right flank of the prey, while lefties attack the left flank (Hori, 1993). This biased attack causes prey fishes to be more vigilant on the side of the body that is attacked more frequently; as a consequence, predation success is decreased in the numerically dominant morph (either lefty or righty) of *P. microlepis* (Hori, 1993). This is a case of negative frequency-dependent selection, and the

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frequency of lefty and righty morphs oscillates around unity (Hori, 1993).

It has been suggested that this morphological laterality in *Perissodus microlepis* is inherited in a Mendelian manner, with a one-locus two-allele model in which the lefty allele is dominant over the righty allele (Hori, 1993; Hori et al., 2007). In addition, the observed segregation ratios indicate the absence of the dominant homozygote. The inheritance of mouth laterality has been examined in other fish species, i.e., *R. flumineus* (Seki et al., 2000) and the Tanganyikan algae-eating cichlid *N. moorii* (Hori et al., 2007), and these studies support the same pattern of inheritance. However, the mechanism responsible for the lack of the dominant homozygote is unclear. This may be due to high mortality in the developmental stage (Seki et al., 2000). To investigate this, we performed laboratory-based breeding experiments and analyzed the segregation ratios and hatchability of each pairing.

Perrisodus microlepis would be the ideal model for such breeding experiments as many ecological studies have examined laterality in this species. However, breeding of this species is highly sensitive to rearing conditions, and we have not yet established a breeding system. We therefore used *Julidochromis transcriptus*, a sponge-eating and substrate-brooding cichlid fish endemic to Lake Tanganyika, in this study. We also conducted cross experiments using *Oryzias latipes*, which is a freshwater fish native to Japan, Korea, and China that has been used as a model organism for developmental and genetics studies (Ozato et al., 1992).

MATERIALS AND METHODS

Fishes

Julidochromis transcriptus individuals were obtained from a commercial vendor in Osaka, Japan. A total of 15 males and 15 females were used for breeding experiments. Sex was determined by examining the form of the outer genital tract under a binocular microscope. Before pairing, all individuals were maintained in aquaria until maturity, reaching a standard length (SL) of at least 5.0 cm.

Wild *O. latipes* were collected from the Kamigamo Experimental Forest Station of Kyoto University, Kyoto, Japan, in May 2004. The sex of individuals was determined by examining the lengths of the anal fins, and mature females and males were kept in separate aquaria.

Crossing scheme and assessment of laterality

The mouth laterality of individuals was checked under a binocular microscope using previously described methods (Seki et al., 2000; Hori et al., 2007). Individuals in which the right side of the head was more developed than the left side, specifically those in which the right joint of the mandible to the suspensorium was positioned frontward and outward compared to the left joint, were classed as righty (Liem and Stewart, 1976). Lefty individuals were the mirror image of righty. Thus, if the mouth opened rightward, the individual was classified as a lefty, and conversely if the mouth opened leftward it was classified as a righty.

The mouth laterality of parents (P_0) was determined prior to the cross experiments. Individuals were anesthetized with 5% phenoxyethanol for a few minutes, and the laterality was determined under a binocular microscope. The fishes were then allowed to recover for two to three days before pairing. After the breeding experiments, the P_0 fish had either died or were anesthetized with 5% phenoxyethanol and preserved in either Davidson solution (deionized water, 347 ml/l; acetic acid, 111 ml/l; ethanol, 320 ml/l; 10% formaldehyde solution, 222 ml/l) or 10% formaldehyde solution, and their laterality was confirmed under a binocular microscope.

The single-pair cross experiments were designed such that at least two replicates were conducted with four combinations of parental lateralities as follows: lefty × lefty (L × L), lefty male × righty female (L♂ × R♀), righty male × lefty female (R♂ × L♀), and righty × righty (R × R). Successful broods, as determined by the number of offspring (≥ 10), were selected from each combination as replicates.

The F_1 individuals were raised until sexual maturity, then anesthetized with 5% phenoxyethanol and preserved in either Davidson solution or 10% formalin, except for individuals used for F_2 test crosses. The laterality of each offspring was judged using the method described above. The standard lengths of F_1 individuals used for the analyses were 1.8–9.5 cm for *J. transcriptus* and 1.2–3.0 cm for *O. latipes*.

F_2 test crosses were conducted to examine the heterozygosity of the lefty individuals and the homozygosity of the righty individuals. To examine heterozygosity of the lefty individuals, pairing was conducted between a lefty F_1 from L × L P_0s and a righty F_1 from R × R P_0s. To examine homozygosity of the righty individuals, pairing was conducted between two righty F_1 from R × R P_0s. Each pairing scheme was conducted in at least two replicates.

F_2 individuals obtained from these parings were raised for more than two months, to ≥ 1.8 cm and ≥ 1.5 cm SL for *J. transcriptus* and *O. latipes*, respectively. Finally, we successfully obtained seven pairs for the test crosses of *J. transcriptus* and five pairs for *O. latipes*. These F_2 individuals were preserved and their laterality was examined using the procedures described above. The segregation ratio was examined using the χ^2 test for goodness of fit to the expected rates based on the Mendelian one-locus two allele model with lefty being dominant over righty, and the dominant homozygote lethal. χ^2 test was conducted on the segregation ratio of every pairs and the total ratio of each cross experiment separately. As a result, no test detected significant difference, excluding the risk of type I error caused by multiple comparisons.

For *J. transcriptus*, pairing was conducted in 50 L (30 × 60 × 36 cm³) or 27 L (30 × 45 × 30 cm³) tanks maintained under a 14/10 h dark/light cycle at 26°C. An artificial nest was made using two slate tiles (10 × 10 × 0.5 cm³) with an entrance width of 3.0 cm (Kohda et al., 2009), and placed in each breeding tank. Females laid all of their eggs on these tiles, and the slate with eggs was carefully transferred to a 3 L aquarium. Dead eggs were counted and removed from the tiles with tweezers every day until hatching. As the egg membrane of *J. transcriptus* is opaque, it was not possible to determine the cause of death, in contrast to the case of *O. latipes* described below. The juvenile fish were fed with live brine shrimp, and thereafter with commercially available flake food (SeraSan®).

Oryzias latipes pairing was conducted in a 1 L tank maintained under a 14/10 h dark/light cycle at 23°C. The eggs were usually collected in the morning soon after the light was turned on. Eggs were removed from the belly of females gently with a small hand net, preserved in a dish with egg water (0.65% NaCl, 0.04% KCl, 0.1% NaHCO₃), and maintained in an incubator at 26°C until hatching. The development of *O. latipes* eggs was checked by eye or under a binocular microscope. Dead eggs were counted and removed from the dish daily, and the dead eggs were divided into fertilized or non-fertilized groups by checking for the presence or absence of a fertilization membrane through the transparent egg membrane. Hatched larvae from each brood were transferred to a 1 L tank and fed commercial powdered food (Ranchuu-kizoku®) and live brine shrimp. Fish were reared and handled in accordance with the Guidelines for Animal Experimentation of Kyoto University.

RESULTS

Morphological laterality in the mouth

All individuals of *J. transcriptus* and *O. latipes* were distinguished as lefty or righty based on whether the mouth
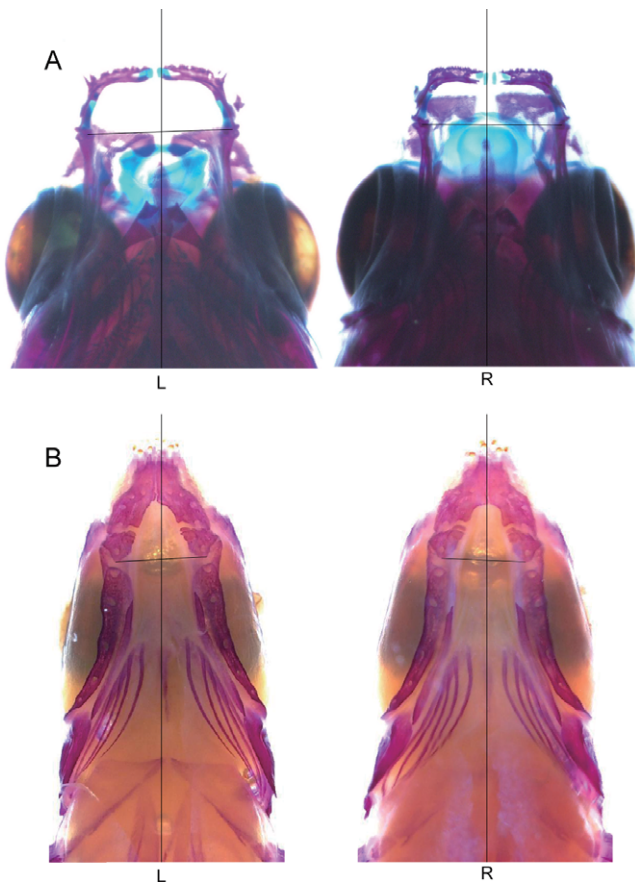
Fig. 1. Ventral view of mouth opening of **(A)** *J. transcriptus* and **(B)** *O. latipes.* In lefty individuals, the mouth opens toward the left, while in righties it does so in the opposite direction. Note that the lines between the right and left ventral corners of the retroarticular do not cross perpendicular to the vertical lines that indicate the mid-lines of the bodies, and that these slant to the left or right in lefty and righty, respectively.

opened leftward or rightward in the ventral view (Fig. 1). With reference to the jaw morphology of *O. latipes* (Werneburg and Hertwig, 2009), the joint of the mandible to the suspensorium is positioned asymmetrically, and the dominant side is placed toward the front and outward.

Egg fertilization ratio and hatchability

Egg fertilization ratios of *O. latipes* were not significantly different in the $L \times L$, $L \times R$, or $R \times R$ P_0s pairing schemes (Table 1; Kruskal-Wallis test, $H = 1.631$, $P > 0.05$), and were > 90% in all crosses.

Eggs of *J. transcriptus* and *O. latipes* normally hatched 2–3 days and 10–12 days after oviposition, respectively. Hatchability did not differ significantly among crossing types in either fish species (Table 2; Kruskal-Wallis test: *J. transcriptus*, $H = 0.887$, $P > 0.05$; *O. latipes*, $H = 2.349$, $P > 0.05$). The hatching rate of the eggs of *O. latipes* from $L \times L$ F_0s was significantly higher than 75% (t-test, $t = 12.3$, $P < 0.001$), the expected ratio based on the hypothesis that homozygosity for the dominant allele was lethal. A total of 156 eggs of *J. transcriptus* did not hatch. The cause of death for *O. latipes* eggs seemed to be non-fertilization, as dead eggs did not have a fertilization membrane and became moldy one or two days after oviposition.

Patterns of inheritance of mouth laterality

In the *J. transcriptus* crossing experiment, the F_1 segregation ratios varied among crossing schemes (Table 3).

Table 1. Fertilization rates (%) in crossing schemes of *O. latipes*.

			O. latipes
P_0 laterality		N	F_1
♂	♀		fertilization rate (%, mean ± SD)
L	L	5	95.7 ± 4.3
L	R	2	90.5 ± 12.0
R	R	1	99.0

N indicates the number of pairs used to observe egg fertilization.

Table 2. Percentages of egg hatchability (%) in each cross scheme of *O. latipes* and *J. transcriptus*.

			O. latipes		*J. transcriptus*
P_0 laterality			F_1		F_1
♂	♀	N	Egg hatchability (%, mean ± SD)	N	Egg hatchability (%, mean ± SD)
L	L	5	93.0 ± 3.3	2	63.2 ± 1.9
L	R	2	85.2 ± 9.8	1	59.7
R	L	2	96.2 ± 1.4	0	–
R	R	3	94.8 ± 4.6	3	70.0 ± 25.2
F_1 laterality			F_2		F_2
L	R	2	75.5 ± 13.2	2	81.6 ± 0.5
R	L	2	68.4 ± 18.7	1	81.3
R	R	3	70.5 ± 3.3	2	56.3 ± 2.5

N indicates the number of pairs.

Table 3. Segregation ratios of F_1 generations in *J. transcriptus*.

Cross (♂ × ♀)	Pair name	n	F_1 L	F_1 R	Observed ratio L:R	Expected ratio L:R	Fit to the expected ratio* Chi-squared	Fit to the expected ratio* P
L × L	J1	54	36	18	2.00:1	2:1	0.042	0.838
	J2	47	32	15	2.13:1	2:1	0.005	0.942
	Total	101	68	33	2.06:1	2:1	0.003	0.960
L × R	J4	113	60	53	1.13:1	1:1	0.111	0.739
	J5	60	30	30	1.00:1	1:1	0.033	0.855
	Total	173	90	83	1.08:1	1:1	0.072	0.788
R × L	J6	44	23	21	1.10:1	1:1	0.000	1.000
	J7	90	43	47	0.91:1	1:1	0.022	0.882
	J8	54	22	32	0.69:1	1:1	0.598	0.440
	J9	57	26	31	0.84:1	1:1	0.079	0.779
	J10	27	15	12	1.25:1	1:1	0.019	0.892
	J11	87	44	43	1.02:1	1:1	0.006	0.940
	Total	359	173	186	0.93:1	1:1	0.169	0.940
R × R	J12	57	0	57	0:1.0	0:1	–	–
	J13	58	0	58	0:1.0	0:1	–	–
	J14	96	0	96	0:1.0	0:1	–	–
	Total	211	0	211	0:1.0	0:1	–	–

* The P value of Chi-square test.

Within each crossing scheme, excluding R × R, the segregation ratio of F_1 was not significantly different between any of the pairs (χ^2 test: L × L, $\chi^2 = 0.003$, $P > 0.05$; L♂ × R♀, $\chi^2 = 0.072$, $P > 0.05$; R♂ × L♀, $\chi^2 = 0.169$, $P > 0.05$). L × L P_0s produced lefty and righty at a ratio of 2:1, L♂ × R♀ P_0s and R♂ × L♀ P_0s produced lefty and righty at 1:1, and

R × R F_0s produced only righty (L:R = 0:1).

In the test crosses between F_1s of *J. transcriptus*, both L ♂ × R ♀ F_1 and R ♂ × L ♀ F_1 produced lefty and righty F_2 at a ratio of approximately 1:1 (Table 4). R × R F_1 produced only righty F_2.

Crossing experiments in *O. latipes* showed a similar pattern to that of *J. transcriptus* (Table 5). Within each crossing scheme, excluding R × R, F_1 segregation ratios were not significantly different among pairs (χ^2 test: L × L, $\chi^2 = 0.166$, $P > 0.05$; L♂ × R♀, $\chi^2 = 0.123$, $P > 0.05$; R♂ × L♀, $\chi^2 = 0.053$, $P > 0.05$). However, the F_1 segregation ratios differed markedly among crossing schemes, and L × L P_0 produced lefty and righty fish at a ratio of 2:1, L♂ × R♀ P_0 and R♂ × L♀ P_0 produced lefty and righty at 1:1, and R × R P_0 produced only righty. In the test cross between F_1, both L♂ × R♂ and R♂ × L♂ F_1 parents produced lefty and righty F_2 at a ratio of 1:1 and R × R F_1 parents produced only righty F_2 (Table 6).

DISCUSSION

The Tanganyikan cichlid *J. transcriptus* and Japanese medaka *O. latipes* show morphological antisymmetry in mouth opening. Consequently, every individual has either a left or right dominant side of the mandible, and its mouth opens either rightward or leftward, respectively. The pattern of laterality appears to follow a type of Mendelian inheritance; the lefty allele is dominant over the righty allele, but there is a lack of fish homozygous for the dominant lefty allele. The same inheritance pattern has been reported previously for laterality in three other fish species (Hori, 1993; Seki et al., 2000; Hori et al., 2007). Therefore, our data are in accordance with the inheritance patterns observed in previous studies, and indicate that this pattern is applicable to a wide range of fishes. Mouth laterality is a qualitative trait in which every individual opens its mouth either leftward or rightward. In fact, asymmetry index calculated by the difference between right and left mandible structure shows discontinuous bimodal distribution in fishes examined to date (Hori, 1991; Mboko et al., 1998; Hori et al., 2007; Takeuchi and Hori, 2008; Yasugi and Hori, 2011). Therefore, this laterality seems to be influenced by a single gene with a major effect.

The absence of the dominant homozygote, which was predicted in a previously proposed inheritance model (Hori et al., 2007), was also suggested by the results of this breeding experiment. However, the cause of this absence was not fully explained by our results that excluded a possible lethal effect in the embryonic stage during which most genes responsible for jaw morphogenesis are expressed (Wittbrodt, 2002), although we cannot exclude the possibility of a lethal effect after hatching.

Alternatively, there may have been cross-incompatibility in this study (Hori et al., 2007). Cross-incompatibility is considered to be the failure of gametes to fuse due to physiological and/or morphological mechanisms (Ballry, 1999), and is widely observed in plants (e.g., Rashid and Peterson, 1992; Matsubara et al., 2003). This mechanism, however, does not fully explain the observed results, as this hypothesis suggests that lefty parents should have produced F_1 with a lefty:righty ratio of 3:1, but this did not occur. In addition, fertilization rates did not change among crossing schemes

Table 4. Segregation ratios of F_2 generations in *J. transcriptus*.

Cross (♂ × ♀)	Pair name	n	F2		Observed ratio	Expected ratio	Fit to the expected ratio*	
			L	R	L:R	L:R	Chi-squared	P
L × R	F2-J1	45	22	23	0.96:1	1:1	0.011	0.916
	F2-J2	23	11	12	0.92:1	1:1	0.022	0.883
	Total	68	33	35	0.94:1	1:1	0.000	1.000
R × L	F2-J3	28	15	13	1.15:1	1:1	0.000	1.000
R × R	F2-J4	29	0	29	0:1.0	0:1	–	–
	F2-J5	27	0	27	0:1.0	0:1	–	–
	Total	58	0	58	0:1.0	0:1	–	–

* P value of Chi-square test.

Table 5. Segregation ratios of F_1 generations in *O. latipes*.

Cross (♂ × ♀)	Pair name	n	F1		Observed ratio	Expected ratio	Fit to the expected ratio*	
			L	R	L:R	L:R	Chi-squared	P
L × L	O1	90	58	32	1.8:1	2:1	0.025	0.875
	O2	32	21	11	1.91:1	2:1	0.031	0.860
	O3	17	11	6	1.83:1	2:1	0.058	0.810
	O4	59	38	21	1.81:1	2:1	0.004	0.949
	O5	34	20	14	1.43:1	2:1	0.175	0.676
	O6	60	41	19	2.16:1	2:1	0.175	0.676
	Total	292	189	103	1.83:1	2:1	0.166	0.684
L × R	O7	157	72	85	0.85:1	1:1	0.386	0.534
	O8	42	23	19	1.20:1	1:1	0.048	0.827
	O8	42	23	19	1.21:1	1:1	0.048	0.827
	Total	199	95	104	0.91:1	1:1	0.123	0.726
R × L	O9	27	15	12	1.30:1	1:1	0.019	0.892
	O10	11	4	7	0.57:1	1:1	0.046	0.830
	Total	38	19	19	1.0:1.0	1:1	0.053	0.819
R × R	O11	54	0	54	0:1.0	0:1	–	–
	O12	35	0	35	0:1.0	0:1	–	–
	Total	89	0	89	0:1.0	0:1	–	–

* P value of Chi-square test.

Table 6. Segregation ratios of F_2 generations in *O. latipes*.

Cross (♂ × ♀)	Pair name	n	F2		Observed ratio	Expected ratio	Fit to the expected ratio*	
			L	R	L:R	L:R	Chi-squared	P
L × R	F2-O1	24	11	13	0.85:1	1:1	0	1.000
	F2-O2	21	12	9	1.3:1	1:1	0.024	0.877
	Total	45	23	22	1.04:1	1:1	0.011	0.916
R × L	F2-O3	18	8	10	0.8:1	1:1	0.000	1.000
	F2-O4	20	10	10	1.0:1.0	1:1	0.100	0.752
	Total	38	18	20	0.90:1	1:1	0.000	1.000
R × R	F2-O5	13	0	13	0:1.0	0:1	–	–
	F2-O6	11	0	11	0:1.0	0:1	–	–
	F2-O7	15	0	15	0:1.0	0:1	–	–
	Total	39	0	39	0:1.0	0:1	–	–

* P value of Chi-square test.

in *O. latipes*. Thus, there appears to be another factor involved in the absence of lefty allele homozygotes. Nevertheless, our results suggest that mouth laterality is regulated by the same genetic factors in *J. transcriptus* and *O. latipes*, as well as other fishes investigated to date (Hori, 1993; Seki et al., 2000; Hori et al., 2007). These results further suggest that the heritable laterality of jaw morphology may be prevalent and maintained by common, simple mechanisms among various fish species. A recent study suggested that morphological laterality is closely associated with behavioral laterality. For example, largemouth bass (*M. salmoides*) showed strong correlations between mouth laterality and their direction of movement during predation (Nakajima et al., 2007). Similarly, the shrimp-eating cichlid fish *N. fasciatus* in Lake Tanganyika shows lateralized hunting behavior related to morphological laterality; i.e., lefty individuals bend their bodies with the right side of the body abutting a rock when aiming at prey shrimp, while righty individuals do the opposite (Takeuchi and Hori, 2008). These studies suggest that laterality in external morphology determines behavioral laterality and is ecologically significant.

In addition, behavioral laterality in the detour direction of Poeciliid fish on encountering an enemy was examined, and the results suggested that laterality seems to have a genetic background (e.g., Bisazza et al., 1998). In fact, in *Girardinus falcatus*, the tendency of left or right turning was shown to be correlated between parents and offspring (Vallortigara and Bisazza, 2002). These examples of behavioral laterality are thought to be caused by brain lateralization. Further studies are necessary to integrate laterality in behavior, external morphology, and the brain, to understand the asymmetry that is ubiquitous in nature and elucidate its inheritance patterns, genetic background, and ecological significance, all of which are poorly understood.

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