

Influence of Hypothyroidism on the Variability of Carotenoid Coloration in *Amatitlania nigrofasciata* Females (Cichlidae)

D. V. Prazdnikov*

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

*e-mail: pdyfish3409@rambler.ru

Received March 1, 2023; revised April 7, 2023; accepted April 17, 2023

Abstract—The study of the effect of thyroid hormones on the development of the pigment pattern, including the expression of sexual dichromatism, contributes to our understanding of the role of endocrine signaling in the evolution of cichlid fishes, one of the most diverse groups of teleosts. This work shows the effect of reduced thyroid hormone signaling on the development of reversed sexual dichromatism in *Amatitlania nigrofasciata*, a Neotropical cichlid in which females, unlike males, have carotenoid coloration. In hypothyroid fishes, there was a slowdown in the rate of metamorphic transformations of the pigment pattern and an increase in phenotypic variability. The adult pattern based on carotenoids began to develop in females only after the completion of treatment of thiourea, which suppresses the synthesis of endogenous thyroid hormones. The data obtained indicate a potentially important role of thyroid hormone-mediated developmental plasticity in the diversification of carotenoid coloration in Neotropical cichlids.

Keywords: thyroid hormones, pigment pattern, phenotypic variability, sexual dichromatism, cichlid fishes

DOI: 10.1134/S0032945223060139

INTRODUCTION

Cichlids (Cichlidae) are characterized by an outstanding variety of pigment patterns among teleosts (Teleostei), which is due to the important role of this morphological trait in the adaptation and speciation of this large group of fishes (Salzburger, 2009; Maan and Sefc, 2013; Ronco et al., 2021).

Carotenoid pigments are responsible for many of the yellow, orange, and red hues in the integument of teleosts and are stored in xanthophores and erythrophores (Sefc et al., 2014). Among Neotropical cichlid groups, there are species with reversed sexual dichromatism, in which females have carotenoid-based coloration that males lack (Tobler, 2007). An outstanding representative of such species are the females of the convict cichlid, *Amatitlania nigrofasciata* (Günther, 1867), which have xanthophore (yellow-orange) patches in the pigment pattern, the color of which is mainly due to carotenoids (Brown et al., 2013; Prazdnikov, 2022). The melanistic pattern due to black-brown melanophores in *A. nigrofasciata* of both sexes consists of eight postcranial vertical bars and a spot on the operculum and usually has little variability (Říčan et al., 2005; Prazdnikov, 2020). Carotenoid coloration in females of *A. nigrofasciata* can perform a signaling function and vary depending on the environment (Beeching et al., 1998; Anderson et al., 2016; Earley et al., 2020).

Thyroid hormones (THs) are important signaling molecules that regulate many ontogenetic processes and act as a link between the environment and phenotypic development in teleosts (Deal and Volkoff, 2020; Lema, 2020). TH signaling coordinates a wide range of morphological development processes, including metamorphosis, mainly due to the binding of the most active THs, triiodothyronine, to nuclear receptors, which leads to changes in gene transcription in different tissues (Blanton and Specker, 2007; Campinho, 2019; Vancamp et al., 2019). THs can affect the development of chromatophores both directly and indirectly by affecting the cascade of intercellular interactions, thereby generating different adult pigment patterns in fishes (Saunders et al., 2019; Parichy and Liang, 2021). For example, in hypothyroid *Danio rerio*, an excess of melanophores develops since their proliferation is not limited, and vice versa, there is a lack of differentiated xanthophores due to a failure of these cells to accumulate the carotenoids necessary for the formation of yellow-orange color, which leads to a change in the melanistic pattern (McMenamin et al., 2014; Saunders et al., 2019).

A similar mechanism is seen in *Andinoacara rivulatus* with reduced TH signaling as adult pigmentation develops, the melanophore population increases and the number of xanthophores decrease dramatically (Prazdnikov and Shkil, 2019a). It was previously shown that TH-deficiency in *A. nigrofasciata* during

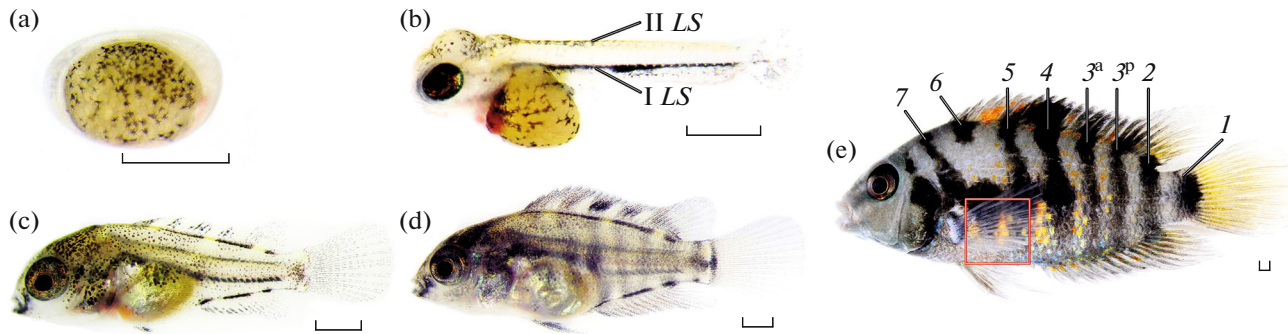


Fig. 1. Development of pigment pattern in *Amatitlania nigrofasciata*: (a) embryo; (b) early larva; (c) late larva; (d) juvenile; (e) adult female. I LS and II LS, larval stripes; 1–7, adult melanistic element (vertical bars); anterior (^a) and posterior (^p) bars; (□) region of the body used to quantify the relative area of melanophore and xanthophore elements. Scale bars: 1 mm.

development leads to an increase in the number of melanistic pattern elements and the absence of sexual dichromatism (Prazdnikov and Shkil, 2019b). However, the formation of carotenoid coloration in females of *A. nigrofasciata* after the suppression of endogenous THs synthesis is canceled poorly understood. Due to the fact that carotenoid coloration may depend on hormonal changes in the melanistic pattern in female Neotropical cichlids (Prazdnikov, 2022), the study of issues related to the effect of THs on the expression of sexual dichromatism contributes to our understanding of the role of endocrine signaling in the evolution of the pigment pattern in cichlid fishes. Here, I investigated the development of carotenoid coloration in *A. nigrofasciata* females reared under hypothyroid conditions to the formation of the definitive melanistic pigment pattern.

MATERIALS AND METHODS

The clutch of fertilized eggs, obtained as a result of the natural spawning of a pair of *A. nigrofasciata*, was divided into two equal groups (80 eggs per group), the embryonic and post-embryonic development of which up to the late larval stage took place under the same conditions. Then the fish were reared in different hormonal regimes: i) euthyroid (control group—natural TH status); and ii) hypothyroid (TH-deficiency). The hypothyroid condition was induced by adding a goitrogen—thiourea ($\text{CS}(\text{NH}_2)_2$) (concentration in water, 0.035%). Thiourea has proven itself in numerous works as a compound that inhibits the synthesis of THs in fish and causes a steady state of hypothyroidism (Blanton and Specker, 2007). The fish were treated with goitrogen until the final formation of the adult melanistic pattern. The concentration thiourea and the stage of initiation of treatment used in this study were chosen on the basis of preliminary optimization experiments (Prazdnikov and Shkil, 2019b). A higher concentration of thiourea ($\geq 0.04\%$) strongly retarded development, including metamorphic transformations, until the formation of the adult pattern

stopped, while a lower concentration of thiourea ($\leq 0.01\%$) did not contribute to noticeable changes in ontogeny and pigment pattern. A 0.035% concentration of thiourea in water always decreased triiodothyronine levels approximately twofold in the hypothyroid group of fish compared to the euthyroid group. One-half of the water from the experimental aquarium was replaced every three days with the addition of thiourea to a predetermined concentration. The rest of the experimental conditions were the same for both groups.

Five stages were distinguished in the development of *A. nigrofasciata*: (i) embryo (fertilization—hatching); (ii) early larva (hatching—complete yolk absorption); (iii) late larva (foraging onset—pelvic fin formation); (iv) juvenile—up to the appearance of sexual dimorphism, and (v) adult fish (Fig. 1). I used days postfertilization (dpf) as a temporal characteristic to compare the timing of ontogenetic events between hormonal groups.

To describe pigment patterning, I used live specimens. Fish were photographed with a Canon EOS 100D digital camera, individuals in the early stages of development—under a Leica MS5 stereomicroscope, and adults—directly in the aquarium. The standard length of fish (*SL*) was measured with an accuracy of 0.1 mm. Pictures of females were taken after the first spawning in each experimental group. This period was considered the end of the formation of carotenoid coloration. The type of chromatophores was identified by the color of the pigment. For the melanistic pattern elements, I used the classification proposed earlier for Neotropical cichlids (Řičan et al., 2005), according to which additional vertical bars, depending on the location, were designated as anterior (^a) and posterior (^p).

In the pigment pattern of females, changes in the number of melanistic elements, as well as the occupied area of xanthophore (yellow-orange) patches on the body, were assessed. Due to the fact that the main population of xanthophores is located in the ventral part of the body of females, a quantitative assessment of the relative area of melanophore and xanthophore

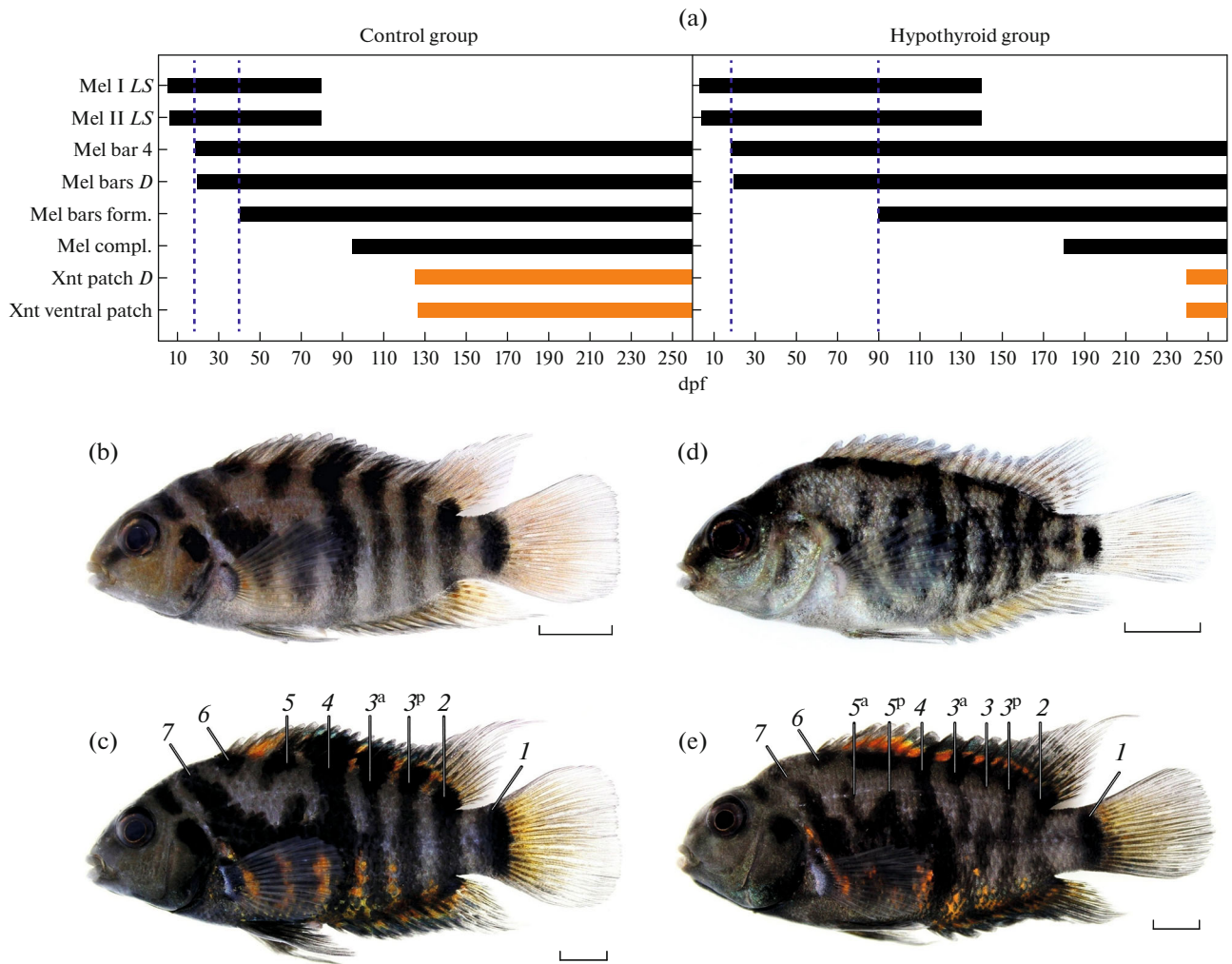


Fig. 2. The sequence of ontogenetic events in pigment patterning (a) and formation of carotenoid pigmentation (b–e) in *Amatitlania nigrofasciata* females reared under different hormonal regimes: (b, c) control group; (d, e) hypothyroid group. D, dorsal fin; Mel, melanophores; Xnt, xanthophores; form., formation of all regions; compl., completion of the pattern development; dpf, days postfertilization; (|) larval–juvenile transition period. See Fig. 1 for other designations. Scale bars: 5 mm.

elements within a specific region was carried out (Fig. 1e), which was determined in the course of previous studies (Brown et al., 2013; Prazdnikov, 2022). Analysis of female pigment pattern elements was performed using the Fiji image processing package and ImageJ 1.8.0 software (Schindelin et al., 2012). Since some groups of fish did not follow a normal distribution, nonparametric Mann–Whitney *U*-tests were conducted.

RESULTS

In the control group of *A. nigrofasciata*, sites of melanophore vertical bars began to form from the late larval stage (Fig. 1c). During the larval–juvenile transition, accompanied by the change of larval elements of the pigment pattern to adult elements, the formation of all regions of the bars occurred, which was completed by 40 dpf (Fig. 1d). The melanistic pigment

pattern on the body, consisting of eight postcranial bars, finally developed by the end of the juvenile stage, by 95 dpf. There were no differences between individuals in the number of bars. Xanthophore patches on the dorsal fin and ventral part of the body began to appear by 124 dpf (Figs. 2a, 2b). The formation of reversed sexual dichromatism in most individuals was completed by 190 dpf (Fig. 2c). The females from the control group were characterized by interindividual variability in the area occupied by melanophore (coefficient of variation 21.18%) and xanthophore (37.51%) elements on the ventral part of the body, as well as in the total area of xanthophore patches on the body (24.10%).

In the hypothyroid group, a slowdown in the rate of larval–juvenile transition was observed (Fig. 2a). The formation of all regions of the vertical bars was completed by 90 dpf. The melanistic pattern finally devel-

Table 1. The frequency of occurrence (FO) of vertical bars on the body of *Amatitlania nigrofasciata* females reared under different hormonal regimes and their standard length (SL)

Number of bars	Group			
	control ($n = 25$)		hypothyroid ($n = 18$)	
	FO, %	SL, mm	FO, %	SL, mm
8	100	46.9 ± 6.6 (38.3–58.4)	11.1	45.4 ± 4.9 (40.5–50.3)
9	0		66.6	41.7 ± 3.0 (38.1–47.1)
10	0		22.3	42.4 ± 2.4 (38.8–45.5)

n —number of fish; for SL , the mean value, standard deviation, and (in brackets) the limits of variation are given.

oped by 180 dpf. The pattern included eight to ten postcranial melanophore bars and patches (Table 1). In fish, the following variants of bar splitting were observed in percentage terms: 1 (12.50%), 3^a (31.25%), 5 (31.25%), 1 and 3^a (6.25%), 3^a and 5 (18.75%). The vertical bars were often fused to each other in the central part of the body (Fig. 2d). The first clusters of xanthophores on the dorsal fin and ventral part of the body appeared in most females 60 days after the completion of thiourea treatment by 240 dpf (Fig. 2a). Xanthophore patches are usually developed in the interbar space and rarely spread to the region occupied by the melanophore bars. The formation of reversed sexual dichromatism in hypothyroid *A. nigrofasciata* was completed by 290 dpf (Fig. 2e). In hypothyroid females, the interindividual variability in the area occupied by the analyzed elements of the pattern was higher than in euthyroid females from the control group; the coefficient of variation for melanophore and xanthophore elements in the ventral part was 23.01 and 47.08%, respectively, and for the total area of xanthophore patches on the body, 50.51%.

Between the two hormonal groups of females, statistically significant differences were found in the area of melanophore and xanthophore elements in the ventral part of the body (Mann–Whitney U test $p < 0.01$) (Fig. 3a), as well as in the total area occupied by xanthophore patches on the body (Mann–Whitney U test $p < 0.01$) (Fig. 3b).

DISCUSSION

The results obtained show that reduced TH signaling in *A. nigrofasciata* led to a slowdown in the rate of metamorphic transformations of the larval pigment pattern into the adult, which, in turn, affected the formation of reversed sexual dichromatism (Fig. 2). In the pigment patterns of females, xanthophore elements began to develop only after the completion of treatment of thiourea, which suppresses the synthesis of endogenous THs. It has previously been shown that hypothyroidism completely suppresses the development of the adult lineage of xanthophores in *A. nigrofasciata* (Prazdnikov and Shkil, 2019b). These data suggest that thyroid hormones may be directly

involved in regulating the cell population of xanthophores in cichlid fishes, probably controlling the state of terminal differentiation and accumulation of carotenoids during the formation of adult patterns similar to that of *Danio rerio* (Saunders et al., 2019).

The formation of melanistic vertical bars in cichlids is associated with extensive dorsal and ventral migration of undifferentiated melanophores in the skin, followed by an increase in density as a result of proliferation and melanin synthesis relative to the interbar space (Řičan et al., 2005; Hendrick et al., 2019; Liang et al., 2020). Changes in the migration of melanophores and their proliferation lead to the merging or splitting of the forming regions of the bars, which in turn causes variability in the number of bars and their position on the body in the adult pattern. An increase in the number of bars in the pattern of hypothyroid *A. nigrofasciata* was most often associated with the splitting of bars 3^a and 5. These vertical bars, along with bars 2 and 4, show variation in development and are responsible for much of the diversity of melanistic patterns in Neotropical cichlids (Řičan et al., 2005, 2016). The global control of pigment cell behavior during pattern formation involves not only THs, but also other hormonal systems connected through the hypothalamic-pituitary pathways (Eskova et al., 2020; Bertolesi and McFarlane, 2021). In this regard, it can be assumed that THs may be involved in the regulation of melanophores through the separation of signaling pathways with other hormones and joint influence on the activity and distribution of these pigment cells.

Expansion of the xanthophore population during the development of carotenoid coloration in *A. nigrofasciata* females seems to be limited to previously formed melanistic elements on the body, as has been shown for hyperthyroid females of this species (Prazdnikov, 2022). The statistically significant differences in the area occupied by xanthophore patches on the body between hormonal groups may be associated with an increase in the number of melanistic elements in the pigment pattern of hypothyroid females. Alterations in TH status in *A. nigrofasciata* lead to an increase in the variability of carotenoid coloration, which can be associated both with the direct hormonal effects on xanthophores and with an indirect effect through a

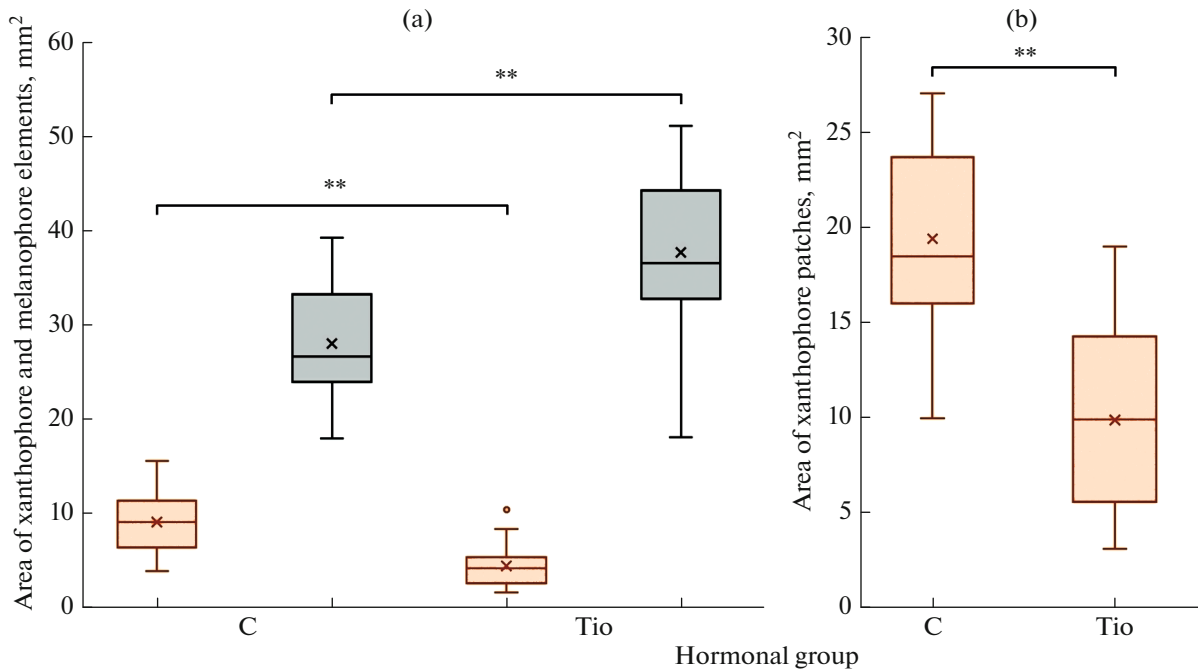


Fig. 3. Relative areas of xanthophore (□) and melanophore (□) pattern elements on the ventral part of the body (a) and total area of xanthophore patches on the body (b) of *Amatitlania nigrofasciata* females reared under different hormonal regimes: C, control group (25 specimens); Tio, hypothyroid group (18 specimens). The box plots show the interquartile range, from 25th and 75th percentile, crosses represent sample means, and the horizontal line crossing the box represents the median values. Whiskers in the box plots denote minimum to maximum values. The circle represents the outlier outside the whiskers. Females were analyzed using a Mann–Whitney *U* test (** $p < 0.01$). Shown are the interquartile range (25–75%), (—) – median, (×) – mean, (└) – minimum and maximum values, (o) – outlier; **differences are significant at $p < 0.01$.

cascade of intercellular interactions and other hormonal systems necessary for the formation of the adult pigment pattern. Changes in the specific of interactions between pigment cells, in particular between melanophores and xanthophores, as well as iridophores, affect changes in the pattern elements and can play an important role in the evolution of teleost pigmentation (Patterson and Parichy, 2019; Salis et al., 2019; Parichy, 2021). The data obtained so far on the development of chromatophores in different cichlid species (Roberts et al., 2017; Hendrick et al., 2019; Liang et al., 2020; Prazdnikov, 2022) indicate both common mechanisms in intercellular interactions similar to other taxonomic groups of fish and distinct mechanisms with a completely different dynamic. Due to the great diversity of pigment patterns in cichlids and their developmental variants, the study of the mechanisms of interaction between pigment cells and endocrine axes in this group of fishes requires further experimental studies.

It is assumed that changes in the relative times of development (heterochrony) and places of chromatophore differentiation (heterotopy) may play an important role in the diversification of pigment patterns in Neotropical cichlids (Prazdnikov and Shkil 2019a, 2019b), *Danio* species (Parichy and Liang, 2021), and guppy species (Prazdnikov, 2021). TH-

induced heterochrony influenced the extent of carotenoid coloration in hyperthyroid females of *A. nigrofasciata* and led to the appearance of phenotypes similar to other Neotropical cichlid species with reversed sexual dichromatism (Prazdnikov, 2022). The absence or decrease in the area occupied by xanthophore patches in the pigment pattern of hypothyroid females of *A. nigrofasciata* is similar to the phenotypic changes in natural populations of females from the genus *Amatitlania*, in which, depending on the reproductive status, as well as increased behavioral interactions with predators and heterospecific competitors, carotenoid coloration can significantly decrease up to its complete absence during the care of offspring (Anderson et al., 2015; Robart and Sinervo, 2018). Taking into account that THs, having a pleiotropic effect, allow teleosts to carry out integrated adaptive phenotypic responses to environmental changes (Lema, 2020), it can be assumed that the TH signaling pathway is involved in the re-allocation of carotenoids between the skin and internal organs.

Hormone-mediated plasticity may contribute to the emergence of novel phenotypes and underlie evolutionary changes in different taxonomic groups of teleosts. For example, alterations in TH signaling have played an important role in the postglacial adaptive radiation of sticklebacks, *Gasterosteus* (Kitano et al.,

2010), the morphological diversification of large African barbs, *Labeobarbus* (Smirnov et al., 2012) and pupfishes, *Cyprinodon* (Lema, 2020), and in the adaptive divergence of the visual system of Midas cichlids, *Amphilophus* (Karagic et al., 2022).

The results of this work, together with previously obtained data on the effect of THs on the formation of coloration in cichlid fishes (Prazdnikov and Shkil, 2019a, 2019b; Prazdnikov, 2022), suggest that hormone-mediated plasticity promotes the emergence of novel developmental variants with the appearance of very different phenotypes and may play an important role in the evolution of the pigment pattern in Neotropical cichlids.

FUNDING

This work was supported by ongoing institutional funding from the Severtsov Institute of Ecology and Evolution Russian Academy of Sciences. No additional grants to carry out or direct this particular research were obtained.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All experimental procedures with fish were carried out following the recommendations described in the Guide for the care and use of laboratory animals (Garber et al., 2011) and ethics approved by the Ethics Committee of the Severtsov Institute of Ecology and Evolution Russian Academy of Sciences dated June 5, 2017, protocol No. 2.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

REFERENCES

Anderson, C., Wong, S.C., Fuller, A., et al., Carotenoid-based coloration is associated with predation risk, competition, and breeding status in female convict cichlids (*Amantitlania siquia*) under field conditions, *Environ. Biol. Fish.*, 2015, vol. 98, no. 4, pp. 1005–1013. <https://doi.org/10.1007/s10641-014-0333-9>

Anderson, C., Jones, R., Moscicki, M., et al., Seeing orange: Breeding convict cichlids exhibit heightened aggression against more colorful intruders, *Behav. Ecol. Sociobiol.*, 2016, vol. 70, no. 5, pp. 647–657. <https://doi.org/10.1007/s00265-016-2085-3>

Beeching, S.C., Gross, S.H., Bretz, H.S., and Hariatis, E., Sexual dichromatism in convict cichlids: The ethological significance of female ventral coloration, *Anim. Behav.*, 1998, vol. 56, no. 4, pp. 1021–1026. <https://doi.org/10.1006/anbe.1998.0868>

Bertolesi, G.E. and McFarlane, S., Melanin-concentrating hormone like and somatolactin. A teleost-specific hypothalamic-hypophyseal axis system linking physiological and morphological pigmentation, *Pigment Cell Melanoma Res.*,

2021, vol. 34, no. 3, pp. 564–574. <https://doi.org/10.1111/pcmr.12924>

Blanton, M.L. and Specker, J.L., The hypothalamic-pituitary-thyroid (HPT) axis in fish and its role in fish development and reproduction, *Crit. Rev. Toxicol.*, 2007, vol. 37, pp. 97–115. <https://doi.org/10.1080/10408440601123529>

Brown, A.C., McGraw, K.J., and Clotfelter, E.D., Dietary carotenoids increase yellow nonpigment coloration of female convict cichlids (*Amantitlania nigrofasciata*), *Physiol. Biochem. Zool.*, 2013, vol. 86, no. 3, pp. 312–322. <https://doi.org/10.1086/670734>

Campinho, M.A., Teleost metamorphosis: The role of thyroid hormone, *Front. Endocrinol.*, 2019, vol. 10, Article 383. <https://doi.org/10.3389/fendo.2019.00383>

Deal, C.K., and Volkoff, H., The role of the thyroid axis in fish, *Ibid.*, 2020, vol. 11, Article 596585. <https://doi.org/10.3389/fendo.2020.596585>

Earley, R.L., Anderson, C.T., Moscicki, M.K., et al., Carotenoid availability and tradeoffs in female convict cichlids, a reverse sexually-dichromatic fish, *Environ. Biol. Fish.*, 2020, vol. 103, no. 12, pp. 1541–1552. <https://doi.org/10.1007/s10641-020-01036-w>

Eskova, A., Frohnhöfer, H.G., Nüsslein-Volhard, C., and Irion, U., Galanin signaling in the brain regulates color pattern formation in zebrafish, *Curr. Biol.*, 2020, vol. 30, no. 2, pp. 298–303. <https://doi.org/10.1016/j.cub.2019.11.033>

Hendrick, L.A., Carter, G.A., Hilbrands, E.H., et al., Bar, stripe and spot development in sand-dwelling cichlids from Lake Malawi, *EvoDevo*, 2019, vol. 10, no. 1, Article 18. <https://doi.org/10.1186/s13227-019-0132-7>

Karagic, N., Härer, A., Meyer, A., and Torres-Dowdall, J., Thyroid hormone tinkering elicits integrated phenotypic changes potentially explaining rapid adaptation of color vision in cichlid fish, *Evolution*, 2022, vol. 76, no. 4, pp. 837–845. <https://doi.org/10.1111/evo.14455>

Kitano, J., Lema, S.C., Luckenbach, J.A., et al., Adaptive divergence in the thyroid hormone signaling pathway in the stickleback radiation, *Curr. Biol.*, 2010, vol. 20, no. 23, pp. 2124–2130. <https://doi.org/10.1016/j.cub.2010.10.050>

Lema, S.C., Hormones, developmental plasticity, and adaptive evolution: Endocrine flexibility as a catalyst for ‘plasticity-first’ phenotypic divergence, *Mol. Cell Endocrinol.*, 2020, vol. 502, Article 110678. <https://doi.org/10.1016/j.mce.2019.110678>

Liang, Y., Gerwin, J., Meyer, A., and Kratochwil, C.F., Developmental and cellular basis of vertical bar color patterns in the East African cichlid fish *Haplochromis latifasciatus*, *Front. Cell Dev. Biol.*, 2020, vol. 8, Article 62. <https://doi.org/10.3389/fcell.2020.00062>

Maan, M.E., and Sefc, K.M., Colour variation in cichlid fish: Developmental mechanisms, selective pressures and evolutionary consequences, *Semin. Cell Dev. Biol.*, 2013, vol. 24, no. 6–7, pp. 516–528. <https://doi.org/10.1016/j.semdb.2013.05.003>

McMenamin, S.K., Bain, E.J., McCann, A.E. et al., Thyroid hormone-dependent adult pigment cell lineage and pattern in zebrafish, *Science*, 2014, vol. 345, no. 6202, pp. 1358–1361. <https://doi.org/10.1126/science.1256251>

- Parichy, D.M., Evolution of pigment cells and patterns: Recent insights from teleost fishes, *Curr. Opin. Genet. Dev.*, 2021, vol. 69, pp. 88–96.
<https://doi.org/10.1016/j.gde.2021.02.006>
- Parichy, D.M., and Liang, Y., Evolution of pigment pattern formation in teleosts, in *Pigments, Pigment Cells And Pigment Patterns*, Singapore: Springer, 2021, pp. 309–342.
https://doi.org/10.1007/978-981-16-1490-3_10
- Patterson, L.B. and Parichy, D.M., Zebrafish pigment pattern formation: Insights into the development and evolution of adult form, *Annu. Rev. Genet.*, 2019, vol. 53, pp. 505–530.
<https://doi.org/10.1146/annurev-genet-112618-043741>
- Prazdnikov, D.V., Effect of thyroid hormones on the development of asymmetric pigment patterns in teleost fish: experimental data on the example of *Amatitlania nigrofasciata* (Cichlidae) and *Poecilia wingei* (Poeciliidae), *Biol. Bull.*, 2020, vol. 47, pp. 198–204.
<https://doi.org/10.1134/S1062359020020065>
- Prazdnikov, D.V., Role of thyroid hormones in color diversity of male guppies: Experimental data on Endler's guppy (*Poecilia wingei*), *Environ. Biol. Fish.*, 2021, vol. 104, no. 6, pp. 675–688.
<https://doi.org/10.1007/s10641-021-01102-x>
- Prazdnikov, D.V., Thyroid hormone signaling in the evolution of carotenoid coloration in Neotropical cichlids with reversed sexual dichromatism, *Ibid.*, 2022, vol. 105, no. 11, pp. 1659–1672.
<https://doi.org/10.1007/s10641-022-01364-z>
- Prazdnikov, D.V. and Shkil, F.N., The experimental heterochronies in a green terror cichlid *Andinoacara rivulatus* (Teleostei: Cichlidae: Cichlasomatinae) indicate a role of developmental changes in the cichlids coloration evolution, *Biol. Bull.*, 2019a, vol. 46, pp. 56–64.
<https://doi.org/10.1134/S1062359019010102>
- Prazdnikov, D.V., and Shkil, F.N., Experimental evidence of the role of heterochrony in evolution of the Mesoamerican cichlids pigment patterns, *Evol. Dev.*, 2019b, vol. 21, no. 1, pp. 3–15.
<https://doi.org/10.1111/ede.12272>
- Řičan, O., Musilová, Z., Muška, M., and Novák, J., Development of coloration patterns in Neotropical cichlids (Teleostei: Cichlidae: Cichlosomatinae), *Fol. Zool.*, 2005, vol. 54, monogr. 1, 46 p.
- Řičan, O., Piálek, L., Dragová, K., and Novák, J., Diversity and evolution of the Middle American cichlid fishes (Teleostei: Cichlidae) with revised classification, *Vertebr. Zool.*, 2016, vol. 66, no. 1, pp. 1–102.
<https://doi.org/10.3897/vz.66.e31534>
- Robart, A.R. and Sinervo, B., Parental response to intruder females altered by ornamentation and mate quality in a biparental fish, *Behav. Ecol.*, 2018, vol. 29, no. 3, pp. 701–710.
<https://doi.org/10.1093/beheco/ary028>
- Roberts, R.B., Moore, E.C., and Kocher, T.D., An allelic series at *pax7a* is associated with colour polymorphism diversity in Lake Malawi cichlid fish, *Mol. Ecol.*, 2017, vol. 26, no. 10, pp. 2625–2639.
<https://doi.org/10.1111/mec.13975>
- Ronco, F., Matschiner, M., Böhne, A., et al., Drivers and dynamics of a massive adaptive radiation in cichlid fishes, *Nature*, 2021, vol. 589, no. 7840, pp. 76–81.
<https://doi.org/10.1038/s41586-020-2930-4>
- Salis, P., Lorin, T., Laudet, V., and Frédérick, B., Magic traits in magic fish: Understanding color pattern evolution using reef fish, *Trends Genet.*, 2019, vol. 35, no. 4, pp. 265–278.
<https://doi.org/10.1016/j.tig.2019.01.006>
- Salzburger, W., The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes, *Mol. Ecol.*, 2009, vol. 18, no. 2, pp. 169–185.
<https://doi.org/10.1111/j.1365-294X.2008.03981.x>
- Saunders, L.M., Mishra, A.K., Aman, A.J., et al., Thyroid hormone regulates distinct paths to maturation in pigment cell lineages, *Elife*, 2019, vol. 8, Article e45181.
<https://doi.org/10.7554/eLife.45181>
- Schindelin, J., Arganda-Carreras, I., Frise, E. et al., Fiji: An open-source platform for biological-image analysis, *Nat. Methods*, 2012, vol. 9, no. 7, pp. 676–682.
<https://doi.org/10.1038/nmeth.2019>
- Sefc, K.M., Brown, A.C., and Clotfelter, E.D., Carotenoid-based coloration in cichlid fishes, *Comp. Biochem. Physiol. Pt. A. Mol. Integr. Physiol.*, 2014, vol. 173, pp. 42–51.
<https://doi.org/10.1016/j.cbpa.2014.03.006>
- Smirnov, S.V., Kapitanova, D.V., Borisov, V.B., et al., Lake Tana large barbs diversity: Developmental and hormonal bases, *J. Ichthyol.*, 2012, vol. 52, no. 11, pp. 861–880.
<https://doi.org/10.1134/S0032945212110082>
- Tobler, M., Reversed sexual dimorphism and courtship by females in the Topaz cichlid, *Archocentrus myrnae* (Cichlidae, Teleostei), from Costa Rica, *Southwest. Nat.*, 2007, vol. 52, no. 3, pp. 371–377.
[https://doi.org/10.1894/0038-4909\(2007\)52\[371:RSDACB\]-2.0.CO;2](https://doi.org/10.1894/0038-4909(2007)52[371:RSDACB]-2.0.CO;2)
- Vancamp, P., Houbrechts, A.M., and Darras, V.M., Insights from zebrafish deficiency models to understand the impact of local thyroid hormone regulator action on early development, *Gen. Comp. Endocrinol.*, 2019, vol. 279, pp. 45–52.
<https://doi.org/10.1016/j.ygcen.2018.09.011>

Publisher's Note. Pleiades Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.