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Morphophysiological development, allometric growth, and initial ontogeny of the Amazonian ornamental characid Moenkhausia oligolepis (Günther, 1864)

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Abstract

This study describes, for the first time, the morphophysiological development, allometric growth patterns, and the main initial ontogenetic events of *Moenkhausia oligolepis*, a species of ecological and ornamental importance in the Amazon region. Hatching occurred 16 hours after fertilization, under an average temperature of 25.36 ± 0.64°C with a pH of 7.28 ± 1.11. From hatching onward, the larvae were sampled at regular intervals (0–6 hours post-hatching with collections every 2 h; 6–22 h every 4 h; and subsequently, daily collections) for morphological, morphometric, meristic, and histological analyses. Larval development spanned from the vitelline stage to the post-flexion stage (0–30 days after hatching—DAH), with a well-defined sequence of events: mouth opening and initiation of exogenous feeding at 3 DAH, cannibalistic behavior at 4 DAH, notochord flexion at 15 DAH (mean CP = 6.33 ± 0.56 mm), and the larval–juvenile transition at 30 POE with the development of fin rays and the appearance of scales. Allometric analyses revealed positive cephalic growth relative to standard length (b = 1.389 for HL/SL), indicating prioritization of the development of structures associated with feeding and sensory perception. Notochord length and preanal distance showed growth close to isometry relative to standard length, while body height exhibited negative allometry. Histological analysis demonstrated progressive differentiation of the digestive tract, with the presence of a buccopharyngeal cavity, esophagus, segmented intestine (anterior, middle, and posterior regions), and mucosal cells at 3 DAH. Cytoplasmic vacuolization was observed in hepatocytes starting at 23 DAH, associated with the presence of digested material in the intestinal lumen. The secondary lamellae of the gills exhibited evident buds at 4 DAH, and the swim bladder was divided into two regions at the end of flexion (22 DAH). Gonadal evaluation indicated undifferentiated gonads up to 50 DAH and ovarian differentiation at 60 DAH, characterized by the presence of primary meiotic oocytes; testicular differentiation was not observed during the analyzed period. Based on the observed morphological and ontogenetic characteristics, four larval stages were described (yolk sac, pre-flexion, flexion, and post-flexion). The results expand knowledge of the species' early biology, providing relevant insights for taxonomic, ecological, and conservation studies, as well as for improving management and larviculture strategies for native ornamental fish.

Introduction

Ontogenetic studies provide information on morphological and physiological changes that occur during the development of organisms, which are directly related to the ecology and survival of species (Baliga and Mehta, 2016). In fish, larval ontogeny is a constantly changing process, in which alterations in ontogenetic state often coincide with changes in diet, microhabitat, behavior, swimming performance, or any combination thereof (Maciel, 2006).

In recent years, scientific interest in understanding the ontogeny of native fish larvae has grown. Understanding the processes that culminate in the development of species is essential for understanding the early life history and biology of the species, for taxonomy (Nakatani et al., 2001) commercial larviculture, and, most importantly, for nutritional management (Portella & Dabrowski, 2008) and reproduction planning, as well as to assist in conservation practices, such as the reintroduction of species into rivers (Maciel, 2006; Azocar et al., 2025). Although larvae of different species may share similarities in the early stages of life (Silva, 2010), the degree of development can vary considerably among them, underscoring the importance of morphological studies for accurate taxonomic identification (Maciel, 2006) and for cultivation in laboratories and fish farms. Furthermore, fish are widely recognized as important indicators of environmental health, especially native species, which play a fundamental role in the early detection of environmental changes, often before more severe damage manifests in the ecosystem (Vieira et al., 2014). These organisms are even more sensitive to environmental variation during the early stages of their life cycle (Ramos et al., 2015), making them particularly effective bioindicators for assessing impacts on aquatic environments.

Despite scientific interest, the available information on morphological and morphometric data for fish larvae and juveniles remains fragmented and unevenly distributed across taxonomic groups, limiting interspecific comparisons and more robust ecological interpretations of the ichthyofauna, as morphological and morphometric changes are consistent with survival needs in the environment (Sala et al. 2005; Devlin et al. 2012). Normal early development and the detection of morphological variations and anomalies are therefore fundamental to understanding the ecological requirements of species (Kovac and Copp, 1999), as well as to identifying factors influencing population recruitment success (Houde, 1994). Data on ontogenetic development are also applicable to improving larval rearing techniques by manipulating environmental parameters and nutritional strategies (Gisbert et al., 2002). According to Gisbert (1999) and Kupren et al. (2014), the morphometric changes observed during the allometric or isometric development of different body regions, associated with locomotion and feeding behavior, constitute relevant parameters for a more precise analysis of larval ontogeny in fish.

Although Brazil is home to an enormous diversity of freshwater fish, only a very small portion of this diversity is used in commercial aquaculture, excluding even important ornamental species (Valenti et al., 2021). This limitation may be related to the scarcity of available information on the reproduction and larval biology of various species, which are fundamental aspects for the development of captive production protocols. In Brazilian aquaculture, exotic species predominate, especially tilapia (*Oreochromis niloticus*), which accounts for the largest share of farmed fish in the country, representing about 70% of all farmed fish (Peixe BR, 2026). In contrast, the share of native species remains proportionally small, despite Brazil's high fish diversity and the economic potential of these resources (Valenti et al., 2021). This scenario highlights the need to expand biological and technological knowledge about native species to support the development of more efficient and sustainable production protocols.

The Neotropical region is home to the world's greatest diversity of freshwater fish, with more than 5,000 species (Reis et al., 2016; Albert et al., 2020; Fricke et al., 2026), distributed mainly within the orders Characiformes and Siluriformes (Eschmeyer, Fricke, and van der Laan, 2018). Among the Characiformes, the family Characidae stands out as the largest and most diverse, with over 1,192 described species (Fricke, Eschmeyer, and Fong, 2019), of which approximately 90% are small to medium in size (Malabarba & Weitzman, 2003). The genus *Moenkhausia*, together with *Astyanax*, *Hemigrammus*, and *Hyphessobrycon*, accounts for 35% of Characidae species (Carvalho et al., 2014) and comprises 116 valid species, widely distributed in freshwater environments of South America (Eschmeyer and Fricke, 2026). The species *M. oligolepis*, known as *lambari, piaba*, or tetra, is widely distributed in South America, primarily in the Amazon Basin and the Guianas (Reis et al., 2016). This species is characterized by a reticulated body, reddish pigmentation on the dorsal margin of the eye, which gives it its common name (fire-eyed tetra), and a dark spot on the caudal fin peduncle (Queiroz et al., 2013; Soares, 2020). It has economic importance, as it is listed among freshwater fish permitted for capture for ornamental purposes (IBAMA, 2012), underscoring the need for

scientific and conservation studies of the species. In this context, although larval development has been described for various species of Characidae, detailed integrative analyses combining morphometry, meristics, allometry, and histology remain scarce for ornamental taxa from the Amazon. This knowledge gap limits both larviculture optimization and the precise identification of early life stages in ecological surveys. Thus, the present study aims to expand knowledge of *M. oligolepis* by describing its larval development, with an emphasis on morphological, morphometric, and histological characteristics. Furthermore, the study seeks to identify critical developmental windows and their implications for larval management, contributing to ontogenetic and taxonomic comparisons and to the optimization of the species' rearing and conservation.

MATERIALS AND METHODS

Ethical Considerations

Collections were conducted in accordance with ICMBio regulations and authorization obtained via the Biodiversity Authorization and Information System – SISBIO (Authorization No. 94406-1), and took place in a natural environment at a previously established location (-4.3316041, -49.0635611) in the city of Jacunda, Pará, Brazil. All experimental procedures followed maintenance and handling guidelines established by the Canadian Council on Animal Care (2005) and the National Council for the Control of Animal Experimentation (CONCEA), with approval from the Animal Use Ethics Committee (CEUA) of the Federal University of Southern and Southeastern Pará (Unifesspa) (Protocol No. 23479.010692/2021-16). The study prioritized animal welfare and minimized stress during the experiments.

Housing of the animals

The fish were kept in two 40-L aquariums, with a density of approximately 1.5 g/L, equipped with continuous artificial aeration and biological filtration, synthetic vegetation, and a constant photoperiod of 12 hours of light and 12 hours of darkness at an average temperature of 25°C. Feeding was performed twice daily until apparent satiety, using commercial feed containing 28% crude protein.

Artificial Reproduction

Five males and four females of *M. oligolepis* were anesthetized with 1 mL of eugenol solution (20 mL of eugenol in 180 mL of 100% alcohol, BIODINÂMICA) diluted in 800 mL of water and then subjected to hormonal induction with crude carp pituitary extract (CPE). To prepare this solution, a 2 mg carp pituitary gland was macerated and diluted in 2 mL of physiological saline (0.9% NaCl). The solution was injected intraperitoneally beneath the pectoral fin of the specimens, in a cephalocaudal direction, using an insulin syringe (0.5 ml) (Dos Santos et al., 2021). Females received two doses of 0.1 mL of CPE, with a 12-hour interval between doses, for oocyte maturation and release, respectively. Spermatogenesis in males was induced by a single dose of 0.05 mL of CPE at the time of the second dose administration to females.

After the injections, the broodstock were kept in 13-liter aquariums with constant aeration, an average temperature of 23.7°C, and a pH of 7.6 for a period of six hours, for reproductive spawning, release, and semi-natural fertilization of the gametes. A mesh screen was placed between the parents and the bottom of the aquariums. This approach is used to prevent the broodstock from ingesting the embryos, as this species lacks parental care. Broodstock used in this experiment were kept in laboratory with the aim of producing new F1 specimens that are raised to adulthood, when they are used in new reproductive experiments.

Experimental Design

Larval hatching occurred 16 hours after fertilization at 23.7°C and pH 7.6. After hatching, the larvae were transferred to three 8-L tanks, maintained under gentle aeration. Larval development was monitored for 30 days after hatching. Larvae were collected at different time intervals, most frequently during the first 24 hours of post-hatching, a period characterized by the most intense morphological changes. During this period, collections occurred at the following intervals: 0–6 hours post-hatching (hph), with sampling every 2 hours (0, 2, 4, and 6 hph), and 6–22 hph, with sampling every 4 hours (10, 14, 18, and 22 hph). Starting on the second day after hatching, collections were performed daily until the end of the experimental period. In each collection, 10 larvae were carefully removed from the aquariums using plastic pipettes for morphological and morphometric analysis, euthanized in a container with 600 mL of water and a lethal dose of Eugenol solution (20 mL of Eugenol in 180 mL of 100% ethanol, BIODINÂMICA), and subsequently fixed in 2.5% glutaraldehyde (0.2 M dibasic phosphate buffer, pH 7.4) for histological analysis. At the end of the experiment, 311 individuals were analyzed, including 40 in the vitelline larval stage, 111 in the pre-flexion stage, 80 in the flexion stage, and 80 in the post-flexion stage. Three days after hatching, when the mouth was already open and the yolk had been reduced, the larvae began to be fed Artemia nauplii (Ocean Star International Inc., USA) three times a day. Food residues and accumulated debris were removed by siphoning in the morning and afternoon. Concurrently, a 30% daily partial water change was performed. During the experimental period, water pH and temperature were monitored, maintaining an average temperature of 25.36 ± 0.64°C and a pH of 7.28 ± 1.11. The system was maintained under a controlled photoperiod of 12 hours of light and 12 hours of darkness.

2.5 Morphological Analysis

An analysis of individuals at each stage was conducted to assess their body morphology. This analysis and larval classification into different stages were based on Ahlstrom & Ball (1954), modified by Nakatani et al. (2001), which consists of: vitelline larvae, pre-flexion, flexion, and post-flexion, following the sequence of development using as the main criterion the level of flexion of the final notochord structure, formation of the fin rays, and their supporting elements. The description of each stage was based on the degree of development and the occurrence of the main morphological events.

- • Vitelline larval stage (LV) – developmental stage between hatching and the onset of exogenous feeding, with the absence of vitellus.

- • Pre-flexion stage (PF) – a developmental stage extending from the onset of exogenous feeding until the onset of notochord flexion, with the appearance of the supporting elements that gave rise to the caudal fin (caudal rays).
- • Flexion stage (FL) – a developmental stage characterized by the onset of notochord flexion, with the appearance of the caudal fin's supporting elements, through to complete flexion, and the appearance of the dorsal and anal fin buds in some species.
- • Post-flexion stage (FP) – a developmental stage characterized by the period from the complete flexion of the notochord and the appearance of the dorsal and anal fin buds until the complete formation of the fin rays.

2.6 Morphometric analyses

The larvae were placed separately in Petri dishes and photographed using a stereomicroscope (LUMEN), a universal adapter (ÓPTICA), and an *iPhone* 12 megapixel camera (Apple Inc., 2019) (Siqueira-Silva et al., 2025). Next, morphometric measurements of the photographed larvae were performed using *ImageJ/FIJI software* (version bundled with 64-bit Java 8). The following body measurements, expressed in millimeters, were recorded: Standard length (SL), eye-to-mouth distance (EMD), eye diameter (ED), head length (HL), head height (HCH), pre-anal length (PreAL), notochord length (CN), body height (ACO), vitelline length (CV), and vitelline height (AV) (Nakatani *et al*., 2001) (**Fig. 1**). For meristic characterization, the total number of myomeres was quantified whenever possible, as well as the rays of the caudal, anal, and dorsal fins (Nakatani, 2001). To assess relative growth patterns among body structures and standard length and head length, allometric relationships were established between each morphometric variable (Y) and the independent variables (X) throughout larval development. The following relationships were analyzed: standard length, head height, eye-to-mouth distance, and eye diameter relative to head length; and head length, head height, notochord length, preanal distance, and body height relative to standard length.

Morphometric relationships were analyzed using simple linear regressions adjusted to data previously transformed by log10, with the aim of linearizing potential-type allometric relationships ($Y = aX^2$) and stabilizing the variance. The log–log transformation converts the power-law model into the linear form $\log(Y) = \log(a) + b \log(X)$, where Y represents the dependent variable, X the independent variable, the regression intercept, and b the slope coefficient, interpreted as the allometric growth exponent.

For each regression, the effective sample size (n), the intercept (a), the slope coefficient (b), the 95% confidence interval for the coefficient b (95% CI), the coefficient of determination (R^2), the p-value of the model, and the p-value of the formal isometry test (H_0: b = 1). The 95% CI for b was calculated from the standard error of the regression, allowing us to assess the precision of the estimate and verify whether the value 1 was contained within the interval. The hypothesis of isometry was formally tested using a t-test applied to the slope coefficient of the linear model. Growth was classified as isometric when b did not differ statistically from 1 ($p \geq 0.05$), positive allometric when $b > 1$ and $p < 0.05$, and negative allometric when $b < 1$ and $p < 0.05$.

The normality of the residuals was assessed using the Shapiro–Wilk test, and homoscedasticity was assessed using the Breusch–Pagan test. The significance level adopted was $\alpha = 0.05$, and all analyses were performed using R software (version 4.2.2).

2.7 Histological processing

The fixed larvae were dehydrated in a series of alcohols of increasing concentration (70%, 80%, and 95%). They were then embedded in resin in three stages: pre-infiltration, infiltration, and embedding. The material was cut into 4-micrometer sections using a manual rotary microtome (LUPETEC, MRP, 2015) equipped with a steel blade (LUPETEC). The histological sections were stained with toluidine blue and subsequently analyzed using an optical microscope (NIKON, ECLIPSE). Photographic documentation was performed using a 12-megapixel iPhone camera (Apple Inc., 2019) (Siqueira-Silva et al., 2025).

Results

3.1 Morphological Analysis

The evaluation of the larval stages of *M. oligolepis* revealed notable characteristics at each stage of development. We monitored the consumption of the yolk sac, the development of the anal pore, the membranous fin, the eyes, the flexion of the notochord, and the fin rays (Table 1).

Table 1
Characterization of the larval stages of *M. oligolepis.* (DAE) days after hatching; (CP) standard length; (mm) millimeters.

STAGES	DAE	SL (mm)	DESCRIPTION
Yolk-fed larval	0–3	1.62–4.13 (3.05 ± 0.87)	After hatching, the larvae still had their mouths closed, heads tilted downward, and exhibited a transparent body, a straight notochord, an embryonic fin, a visible preanal pore, and an adhesive gland on the dorsal region of the head; the yolk sac was voluminous, oval, and yellowish in color. Ten hours after hatching, chromatophores—isolated pigment cells—were observed at the edge of the yolk sac. Around 14 hours, slight pigmentation appeared in the anterior part of the eyes, and by 22 hours, this pigmentation had encircled the optic vesicle and appeared in small amounts on the dorsal part of the body. Two days after hatching, the eyes were pigmented, the pectoral fins were already visible, and the mouth was open. Three days after hatching, pigmentation intensified at the edge of the yolk, the dorsal part of the body, and the region of the swim bladder, which was beginning to inflate. (**Fig. 2A-B**).
Pre-flexion	4–14	3.33–6.21 (4.25 ± 0.47)	They had an open mouth and fully pigmented eyes; the yolk sac was already completely absorbed, and the pectoral fin was present and functional. Chromatophores were distributed throughout the body, including the swim bladder and the operculum region. The main visible structures were the preanal pore, the embryonic fin, the straight notochord, and the swim bladder. (**Fig. 2C-D**).
Flexion	15–22	5.33–7.74 (6.33 ± 0.56)	Beginning with the appearance of caudal fin rays, pigmentation is distributed across the body and head, in the swim bladder, and in the operculum region. Visible structures included the preanal pore, the embryonic fin, and the slightly flexed notochord. At 20 days of post-hatching, the notochord was even more flexed. At 21 days, a reduction in the membranous fin was observed, along with the presence of anal fin rays and the swim bladder divided into two regions, as well as the presence of chromatophores in the caudal fin. (**Fig. 2E-F**).
Post-flexion	23–30	6.41–10.0 (8.01 ± 0.89)	Presence of the pectoral fin, as well as the rays of the caudal, anal, dorsal, and pelvic fins. Emergence of the adipose fin at 28 days and initial appearance of scales at 30 days. Pigmentation was widely distributed throughout the body, with increased numbers of chromatophores. Visible structures included the preanal pore, a fully flexed notochord, which became less visible due to its transparency, and a further reduction of the embryonic fin, with the swim bladder divided into two regions. (**Fig. 2G-H)**.

The main events of early development are summarized in Fig. 3. It presents the temporal sequence of ontogenetic milestones over the days following hatching, associated with the average standard length and larval stages. Hatching occurred on day 0, with larvae exhibiting an average standard length of 1.7 mm, in the vitelline stage. On the second day after hatching, active swimming was observed, accompanied by the development of the pectoral fin and inflation of the swim bladder. The onset of exogenous feeding occurred on the third day after hatching, concurrent with mouth opening and the reduction of the yolk sac. Cannibalistic behavior was observed starting on the fourth day after hatching, coinciding with the onset of the pre-flexion stage. The acquisition of caudal propulsion occurred 15 days after hatching, at which time notochord flexion began, and the caudal fin rays emerged, with an average standard length of approximately 6.0 mm during the flexion stage. Improved hydrostatic control was recorded around the 22nd day after hatching, with the differentiation of the swim bladder into two regions, near the end of the flexion stage. At the beginning of the post-flexion stage, the larvae reached an average standard length of approximately 6.8 mm, and at the end of the stage, around the 30th day after hatching, the larva–juvenile transition occurred, associated with fin development and the onset of scale formation, with an average standard length of 8.0 mm (**Fig. 3**).

3.2 Morphometric analyses

Morphometric data on the larval development of *M. oligolepis* showed progressive growth of body structures throughout the larval stages, from the vitelline larval stage to the post-flexion stage, with the exception of the yolk sac, which was no longer present starting from the pre-flexion stage. **(**Table 2**).**

Table 2
Morphometry of *Moenkhausia oligolepis* larval structures. Data are presented as mean and standard deviation.

Variables (mm)	Yolk-fed (n: 40)	Pre-flexion (n: 111)	Flexion (n: 80)	Post-flexion (n:80)
CP	3.055 ± 0.870	4.256 ± 0.471	6.333 ± 0.563	8.011 ± 0.899
CC	0.491 ± 0.255	1.021 ± 0.146	1.445 ± 0.146	1.907 ± 0.269
ACB	0.520 ± 0.218	0.761 ± 0.099	1.153 ± 0.169	1.405 ± 0.106
DO	0.184 ± 0.113	0.322 ± 0.045	0.511 ± 0.074	0.685 ± 0.094
OB	0.139 ± 0.089	0.250 ± 0.089	0.336 ± 0.050	0.422 ± 0.078
CV	0.569 ± 0.135	—	—	—
AV	0.392 ± 0.085	—	—	—
PreAL	1.722 ± 0.366	2,169 ± 0.307	3,440 ± 0.319	4,194 ± 0.440
CN	2.889 ± 0.790	3.933 ± 0.444	5.896 ± 0.537	7.080 ± 0.784
ACO	0.458 ± 0.161	0.628 ± 0.129	0.887 ± 0.097	0.989 ± 0.198

Legend: (SL) standard length; (HL) head length; (HW) head width; (ED) eye diameter; (OB) eye-to-mouth distance; (CV) vitelline length; (AV) vitelline height; (PreAL) preanal length; (CN) notochord length; (ACO) body height; (N) sample number; (mm) millimeters.

The meristic data revealed variations in the number of structural elements throughout the larval development of *M. oligolepis*, based on the counting of myomeres and fin rays. The number of myomeres could be clearly observed in the early stages, when the high body transparency allowed visualization of the

muscle segments. However, as development progressed, the ability to count these elements was compromised due to the gradual loss of transparency and thickening of the musculature, which made it difficult to distinguish them individually. In contrast, the number of fin rays showed a progressive increase throughout the larval stages. The observed pattern demonstrates sequential development of the meristic elements **(**Table 3**)**.

Table 3
Minimum and maximum ranges of meristic characters in *Moenkhausia oligolepis* larvae throughout the developmental stages.

Meristic characteristics	**Yolk-fed larva**	**Pre-flexion**	**Flexion**	**Post-flexion**
Number of myomeres	26–32	25–38	23–34	15–25
Caudal fin rays	—	—	05–19	21–24
Anal fin rays	—	—	06–07	09–18
Dorsal fin rays	—	—	—	04–18

Table 4. Parameters of allometric regressions for morphometric relationships in *Moenkhausia oligolepis* larvae

Morphometric relationship	*a*	*b*	Growth type	95% CI(b)	R^2	*p*	*n*
CC vs. OB	-1.377	0.736	Negative allometry	0.683 - 0.789	0.716	<0.001	301
CC X DO	-1.045	0.924	Negative allometry	0.882 - 0.965	0.865	<0.001	301
CC vs. ACB	-0.189	0.763	Negative allometry	0.738 - 0.788	0.921	<0.001	311
CP vs. CC	-2.162	1.389	Positive allometry	1,329 - 1,448	0.874	<0.001	311
CP vs. ACB	-1,971	1.139	Positive allometry	1,104 - 1,117	0.930	<0.001	311
CP vs. CN	0.005	0.945	Negative allometry	0.933 - 0.957	0.988	<0.001	311
CP X PreAL	-0.945	0.945	Negative allometry	0.921–0.969	0.952	<0.001	311
CP vs. ACO	0.865	0.866	Negative allometry	0.820–0.910	0.822	<0.001	311

Legend: a: intercept; b: growth coefficient; 95% CI(b): 95% confidence interval for lower and upper b; R^2: coefficient of determination; p: significance level; n: number of larvae analyzed. (PL) standard length; (HL) head length; (HHL) head height; (ED) eye diameter; (OB) eye-to-mouth distance; (CV) vitelline length; (AV) vitelline height; (PreAL) preanal length; (CN) notochord length; (ACO) body height.

3.3 Body proportions

The morphometric relationships analyzed showed a significant fit to the potential model, evidenced by high coefficients of determination and p-values less than 0.001. The estimated parameters of the allometric regressions are presented in Table 3.

Ontogenetic allometric analysis revealed distinct growth patterns among the cephalic and body structures of *M. oligolepis* larvae. The relationships between head length (CC) and eye–mouth distance (OB) (b = 0.736), as well as between head length and head height (ACB) (b = 0.763), showed negative allometry, indicating that these structures grew proportionally less than head length. In contrast, eye diameter (ED) (b = 0.924) showed growth close to isometry, indicating a more proportional growth rate relative to head length (**Fig. 4**).

Regarding standard length (SL), the results showed positive allometry for head growth. The relationship between head length and standard length showed a high coefficient (b = 1.389), indicating that the head grows faster than the body. Similarly, head height relative to standard length also exhibited positive allometry (b = 1.139) **(Fig. 5)**. On the other hand, body structures such as notochord length (CN) (b = 0.945) and preanal distance (PreAL) (b = 0.945) showed growth close to isometry, suggesting development proportional to body length. The exception was body height (ACO), which exhibited negative allometry (b = 0.866), indicating proportionally slower growth relative to standard length (**Fig. 5**).

3.4 Histological Analyses

During the early stage of larval development of *M. oligolepis*, structures such as myomeres, notochord, a voluminous yolk sac, brain, and a rudimentary heart in the pericardial cavity anterior to the yolk sac were observed. The optic vesicle had already invaginated, forming the optic cup as well as the lens **(Fig. 6A)**. A straight, simple tube was also present in the ventral region of the larva, representing the rudiment of the primitive digestive tract. It was undifferentiated, with tissue similar to and continuous with the integument, penetrating directly into the posterior part of the yolk sac at the time of hatching **(Fig. 6B)**. As development progressed, it was observed that the digestive system was differentiated by 3 DAE, featuring a buccopharyngeal cavity, small initial teeth, an esophagus, and an intestine. The mouth, pharynx, and anus became completely open, and the esophagus—a short, narrow tube continuous with the buccopharyngeal cavity—connected to the intestine (**Fig. 6C**).

Sensory structures and those related to swimming and respiration, such as the nostril, eyes pigmented by chromatophores and their complete cellular layers, an inflated swim bladder, and gill arches located beneath the operculum, were more clearly defined, with evidence of secondary lamellae (**Fig. 6C).** The esophageal epithelium exhibited mucous or secretory cells, and the liver was also present (**Fig. 6D**). The primary lamellae were developing, showing buds for

the development of secondary lamellae at 4 DAE (**Fig. 6E**). As development progressed, new teeth originating from the buccal epithelium emerged, and the inflated swim bladder was divided into two regions. The intestinal epithelium exhibited brush borders, and the presence of digested material was observed in the intestine. There was expansion of the digestive tract, with increased capacity for food passage, and the intestine was divided into anterior, middle, and posterior segments (**Fig. 6F**), with the presence of mucus-secreting goblet cells to facilitate food transport and protect the mucosa of the intestinal folds (**Fig. 6G).** Goblet cells were also present in the esophagus (**Fig. 6H**). Hepatic vacuolization is notable (**Fig. 6I**) compared to an earlier stage (**Fig. 6D**), which may indicate increased metabolic activity associated with the functional reorganization of the liver. Subsequently, the secondary lamellae were already present (**Fig. 6J**). With the development of the larvae's vision, it is possible to observe the outermost pigment layer, optic nerve, lens, and vitreous body at 23 DAE (**Fig. 6K**).

In *M. oligolepis* juveniles up to 50 days post-hatch (DPH), the gonads were undifferentiated, consisting of somatic components, germ cells, and blood vessels (**Fig. 7A**). The somatic cells had a pavement-like, elongated morphology, with a basophilic nucleus and sparse cytoplasm. The primordial germ cells (PGCs) were oval in shape, with a voluminous, irregular nucleus occupying a large portion of the cell volume (**Fig. 7A**), containing euchromatin, as well as a single, distinct nucleolus (**Fig. 7C**). The PGCs were organized into continuous, aligned strands, surrounded by somatic cells forming the gonadal primordium (**Fig. 7B**). At 60 DAE, the first sign of gonadal differentiation was observed with the presence of primary oocytes, indicating the onset of ovarian oogenesis (**Fig. 7D–G**). They were organized into clusters (**Fig. 7H and I**).

Discussion

In the yolk-fed larval stage, immediately after hatching, the size of the newly hatched larvae (3.05 ± 0.87 mm) is relatively similar to that observed by Dos Anjos (2006) (2.9 ± 0.2) in the cardinal tetra (*Paracheirodon axelrodi*) and by Stevanato and Ostrensky (2018) (2.99 ± 0.32) in the tetra *Astyanax lacustris*, tetras, from the same family as *M. oligolepis*. The larvae have a transparent body and lack functional mouths and intestines, in addition to having little pigmentation in the eyes, similar to what is observed in most larvae of Neotropical freshwater fish (Nakatani et al., 2001). Despite this, small pigments formed by dendritic chromatophores can be observed, scattered along the outer edges of the yolk sac. The pigmentation pattern, when combined with morphometric and meristic data in fish larvae, is a valuable tool for the taxonomic identification of species, as it serves as a distinctive character used to differentiate between species (Simon & Vondruska, 1991; Meijide & Guerrero, 2000). According to Nakatani et al. (2001), most fish species in the Order Characiforms exhibit a relatively similar post-hatching morphological pattern, appearing underdeveloped and transparent. This characteristic is important for the animal at this stage, as it represents a survival strategy to avoid predation and ensure survival. As development progresses, body pigmentation increases (Almeida, 2016).

During the vitelline larval stage, the voluminous yolk sac serves as the primary endogenous nutrient source until the onset of exogenous feeding (Govoni et al., 1986). Once the yolk sac is depleted, individuals must find food in the environment to survive (Ferreira et al., 2009). In most fish species, larvae have a simple, undifferentiated digestive tract, with digestive organs developing later (Govoni et al., 1986). This can be observed in *M. oligolepis* larvae, which exhibited a primitive, simple digestive tract. Subsequently, with the depletion of the yolk, the digestive tract appeared more developed, consisting of anterior, middle, and posterior regions. Larvae that hatch with a large amount of yolk and an undifferentiated digestive tract, such as *M. oligolepis*, are classified as altricial (Onal et al., 2010). Altricial larvae are those with limited yolk reserves, which are depleted within the first few days after hatching, causing the larvae to begin exogenous feeding even while the digestive system is still developing (Holt et al., 2011), a characteristic typical of underdeveloped larvae (Fuiman and Werner, 2009). In larvae of viviparous fish such as *Poecilia vivipara*, embryonic development occurs within the maternal ovary and nutrition is lecithotrophic (Wourms et al., 1988; Arcanjo et al., 2014). The yolk sac is progressively consumed throughout embryogenesis, being reduced or practically absent at birth (Arcanjo et al., 2014). At this stage, the digestive system is already relatively well-differentiated, with an open mouth and anus, an intestine with a defined lumen, and recognizable associated digestive glands, allowing for the immediate onset of exogenous feeding (Infante and Cahu, 2001; Arcanjo et al., 2014).

An important structure present in the vitelline larval stage of *M. oligolepis* is the adhesive gland, located in the upper region of the head. According to Godinho et al. (2003), in natural environments, this gland helps the larvae remain near the hatching site, even when carried by water currents, contributing to their more efficient and controlled dispersal, as well as their maintenance in a more nutritious environment. This gland is no longer present four days after hatching. In *Astyanax mexicanus*, it has been demonstrated that the adhesive gland exerts an inhibitory role on swimming, favoring adhesion to the substrate and reducing energy expenditure, an effect that disappears after its ontogenetic regression (Pottin et al., 2010). This regression coincides with increased swimming ability and hydrostatic control, due to the complete differentiation of pectoral fins and eyes in *M. oligolepis*, which are essential for exploring the water column (Fuiman & Werner, 2009; Pottin et al., 2010) and for foraging in the environment. Thus, the loss of this structure indicates a functional transition to a more active lifestyle, compatible with the occupation of the water column and the need for greater mobility in the aquatic environment. The onset of active swimming and the inflation of the swim bladder observed in this study follow the pattern described for teleost and Characiforms, in which these structures are directly associated with improved hydrostatic control and the exploration of the water column (Blaxter, 1988; Nakatani et al., 2001).

At the beginning of the pre-pharyngeal stage, the optic vesicle exhibits significant morphological development, with its ocular layers already formed. The opening of the mouth, the formation of the digestive system, the opening of the anus, the presence of an inflated swim bladder, the nasal fossa, and the development of the pectoral fin are events that occur almost simultaneously. The development of these structures improves directional control, balance, and swimming control (Trotter et al., 2003), increases efficiency in food capture and predator evasion (Osse & Van den Boogaart, 1999) and, consequently, ensures the survival of the larvae (Stevanato and Ostrensky, 2018). The presence and functioning of sensory organs are fundamental in this context.

Given the central role of the eyes in visual perception, their pigmentation and the consequent development of visual acuity become priorities during larval development (Moorman, 2001). In this context, the presence of the lens (a spherical structure) in the eyes of *M. oligolepis* larvae maximizes their refractive power. Furthermore, its anterior position within the eyeball provides a greater focal length, facilitating the convergence of light rays onto the retina and

contributing to the formation of sharper images in the aquatic environment (Romer and Parsons, 1986). According to Lasker et al. (1970), the pigmentation of the eyes, concurrent with the opening of the mouth and intestine, associated with larval growth, is directly related to the larvae's preparation to receive exogenous food, which highlights the importance of synchrony in the formation of these structures and the rapid consumption of yolk.

According to Osse and van den Boogart (2004), faster head growth is typical of many fish. Such development is vital for feeding and exhibits priority growth in many teleost groups, helping newly hatched larvae to establish exogenous feeding (Peña and Dumas, 2009; Gao et al., 2015). In *M. oligolepis*, head length and depth exhibited positive allometric growth, indicating differentiation and rapid development of neural structures such as the midbrain and hindbrain, sensory structures (free neuromasts, vision, and olfaction), respiratory structures (gill apparatus), and feeding organs (mouth, hyoid bone, and mandibular structures). The increase in cephalic structures such as eye diameter, eye-to-mouth distance, head length, and head height observed in this study suggests a greater capacity for perception and response to the environment (Maciel, 2006), as well as a reaction to light stimuli, finding and obtaining prey, detecting potential predators, and successfully completing the transition from endogenous to exogenous nutrition (Peña and Dumas, 2009; Wang et al., 2019). In *M. oligolepis*, eye diameter (ED), notochord length (NL), and preanal length (PreAL) exhibited growth approaching isometry. These results support the hypothesis of ontogenetic growth priorities (Osse & van den Boogaart, 1990), whereby structures associated with primary functions, such as vision and locomotion, tend to maintain proportional growth during larval development, indicating the functional maintenance of these structures throughout larval ontogeny. Body growth may be related to the development of myomeres, the vertebral column, the digestive tract, and associated glands, which aid in locomotion and metabolism (Gao et al. 2015; Saemi-Komsari et al. 2018). It is well known that the complete resorption of the yolk, which also marks the onset of the exogenous feeding stage, is one of the most vulnerable points in larval development, with high mortality rates, as observed by Kamber (1992), Nunn (2012), and Stevanato and Ostrensky (2018). *M. oligolepis* larvae in the pre-flexion stage are in the transition phase between endogenous and exogenous feeding.

The early presence of mucus-producing cells in the esophageal epithelium of *M. oligolepis* larvae at the 3rd DAE suggests that the esophagus is already morphologically prepared to provide protection against potential mechanical damage caused by food ingestion (Galvão et al., 1997), as mucous cells produce mucus that lubricates the organ's surface against abrasion and epithelial injury (Anderson, 1986). Cytoplasmic vacuolization in the hepatocytes of *M. oligolepis* larvae suggests an intensification of hepatic metabolic activity associated with exogenous feeding, an indicator of functional maturation of the liver related to the storage and processing of lipids and carbohydrates (Marthinsen et al., 2026). Some authors have reported that hepatocytes exhibit glycogen storage activity during the larval stage (Hamlin et al., 2000; Peña et al., 2003; Micale et al., 2006). According to Hamlin et al. (2000), this storage capacity can be considered an indicator of the onset of hepatocyte functionality, which persists throughout the larval and juvenile stages. In *M. oligolepis* larvae, hepatocyte differentiation in the liver indicates the structural formation of the organ and may be associated with the onset of its functional activity.

At the flexion stage, 15 days after hatching, the larvae have a CP of 6.33 ± 0.56 mm and the notochord is already flexed. Similar values were observed in other small Characiforms, such as in *Moenkhausia cf. gracilima*, with notochord flexion occurring on average at 5.91 mm (Santos et al., 2017); in the *charutinho Pyrrhulina australis*, with flexion between 5.3 and 7.3 mm (Taguti et al., 2009); and in the *lambari*-do-campo *Markiana nigripinnis*, with an average of approximately 7.0 mm (Souza et al., 2023). Notochord flexion is one of the main criteria for defining larval stages in teleosts and is directly associated with the reorganization of the axial axis and the differentiation of the caudal complex (Kendall et al., 1984; Ahlstrom et al., 1976), leading to the acquisition of caudal fin propulsion with greater locomotor performance (Flammang & Lauder, 2009).

The rays of the caudal and anal fins were the first to develop, followed by the rays of the dorsal, pelvic, and pectoral fins, and finally the adipose fin. The sequence of fin development observed in *M. oligolepis* is similar to that of other Characiformes, such as the sardines *Triportheus albus* and *T. angulatus* (Cajado et al., 2023). The formation of anal fin rays before the dorsal fin is not a characteristic shared by all members of the Characidae family, and in some species, the dorsal fin appears during development before the anal fin, as in the lambari *Moenkausia cf. gracilima* (Santos et al., 2017), in the field lambari *Markiana nigripinnis* (Souza et al., 2023), and in the Green Tetra *Heterocharax macrolepis* (Mattox, 2014), this being a more common pattern of emergence in Characidae. With the formation of these structures, partial resorption of the membranous fin was observed. Fin development is a fundamental aspect during the early ontogeny of fish, as it is directly associated with changes in swimming mode and speed, feeding strategies, and the ability to escape predation (Kendall et al., 1984; Osse & van den Boogaart, 1999).

In the post-flexion stage, an intensification of body pigmentation is observed, and the larvae begin to exhibit a morphology more similar to that of adult individuals. With growth and the progressive development of structures, efficiency in swimming and food capture becomes comparable to that of adult fish. This functional advancement is corroborated by the greater degree of coiling of the digestive tract in *M. oligolepis*, indicating greater digestive capacity and adaptation to exogenous feeding. The anatomical characteristics of the digestive system in fish are closely related to the nature of the food, habitat conditions, nutritional status, and the organism's stage of development (Seixas Filho et al., 2001). According to Balon (1975), the rapid initial development of body structures promotes intense morphological and physiological changes; however, as ontogeny progresses, this rate tends to slow down progressively.

In teleost fish, primordial germ cells migrate from extragonadal regions toward the gonadal ridge, where the gonadal primordium is established and the process of differentiation of male or female reproductive organs begins (Braat et al., 1999). In the present study, the gonadal primordium was identified in *M. oligolepis*; however, no gonadal differentiation was observed in individuals up to 50 days post-hatch (DPH), since the gonadal tissue lacks evident histological organization and is characterized by the presence of PGCs.

The gonadal primordium progressively increases in length due to the mitotic proliferation of its cells, giving rise to an undifferentiated gonad that undergoes a series of structural modifications responsible for the formation of the female or male gonad (Yamamoto, 1969; Devlin & Nagahama, 2002). In this study, ovarian tissue differentiation was observed at 60 DAP. This process may have occurred between 51 and 60 DAP. On the other hand, testicular differentiation was not identified during the analyzed period. Similar results have been described for another species of the Characidae family. In *Astyanax altiparanae*, ovarian and testicular differentiation occur, respectively, at 58 and 73 days after hatching (Adolfi et al., 2015). In another species of Characiformes, *Brycon orbignyanus*, a medium-sized species, ovarian differentiation also occurs prior to testis formation, at three and five months of age, respectively (Quirino et al., 2022). In the chameleon goby, *Tridentiger trigonocephalus*, belonging to the family Gobidae, initial ovarian differentiation was recorded at 55 days post-

hatching (DAE), while testicular differentiation began at 65 DAE (Cho et al., 2014). In most gonocoric teleost species, the ovary develops first, while in males the gonad remains undifferentiated for an additional period, which can range from days to weeks or even months before the onset of testicular formation (Nakamura et al., 1998; Devlin, 2002). This pattern of sexual differentiation in males may explain the absence of differentiated testes during the analyzed period.

The detailed morphological characterization performed in this study, in addition to expanding the ontogenetic understanding of *Moenkhausia oligolepis*, provides insights applicable to the larval management of the species, since the delineation of developmental stages is fundamental for adjusting feeding practices, such as determining the appropriate timing of introduction and the size of live feed (Hunter, 1984; Rotta, 2003). The cannibalism observed during larval development may be associated with growth heterogeneity among individuals. Initial size differences favor the predation of smaller individuals by their larger conspecifics, intensifying mortality within the batch, a pattern reported for other species (De Angelis et al., 1980; Hecht and Appelbaum, 1988; Baras, 1998; Baras, 2000; Kestemont et al., 2003). Although size sorting is suggested as a strategy to reduce cannibalism (Hecht and Pienaar, 1993), its application during the larval stage is limited due to the difficulty of handling individual organisms.

This study reinforces the importance of integrating morphological, morphometric, and histological analyses to understand larval development in fish. Identifying structural variations throughout ontogeny allows us to infer possible ecological adaptations related to habitat transitions, changes in feeding patterns, and behavioral adjustments during the early stages of life.

Concluding Remarks

The larval development of *M. oligolepis* exhibits a well-defined ontogenetic sequence, with morphological, morphometric, and histological events directly related to the transition from endogenous to exogenous feeding and the progressive acquisition of sensory and locomotor capabilities. Allometric growth patterns indicated preferential growth of the cephalic region, highlighting the importance of the development of structures associated with feeding and the visual system. Histological analysis confirmed the functional differentiation of the major organs. Based on the observed characteristics, four larval stages were defined (yolk-fed, pre-flexion, flexion, and post-flexion), contributing to the understanding of the species' early biology and providing insights for taxonomic, ecological, and conservation studies, as well as for the improvement of larviculture techniques for native ornamental fish. Histological analyses revealed ovarian differentiation at 60 days post-hatch (DPH), while testicular differentiation was not observed during the analyzed period, indicating that it requires a longer ontogenetic development time in this species.

Declarations

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Competing interests' statement

The authors declare no conflict of interest.

Author Contributions

VCC: Conceptualization; Data curation; Investigation; Methodology; Visualization; Roles/Writing - original draft. ESNA: Data curation; Investigation; Visualization; Roles/Writing; EJSF: Data curation; Investigation; Visualization; Roles/Writing; OAL: Data curation; Investigation; Visualization; Roles/Writing; BLS: Data curation; Visualization; JR: Data curation; Visualization; CM: Investigation; Methodology; CM: Data curation; Visualization; DHSS: Conceptualization; Methodology; Formal analysis; Project administration; Resources; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Data Availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

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Figures

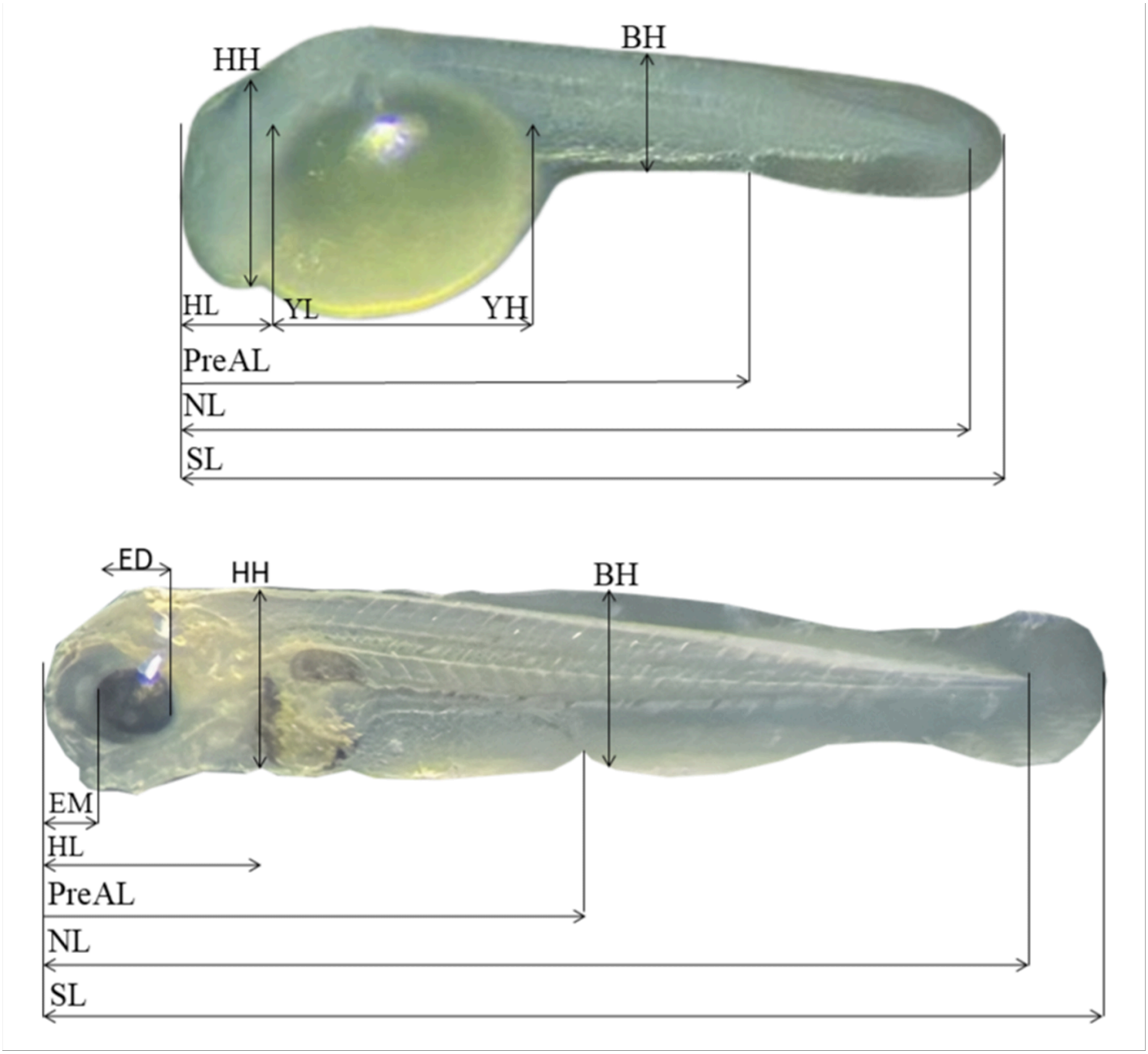


Figure 1

Schematic diagram of morphometric measurements of *Moenkhausia oligolepis* larvae. Standard length (SL), eye-to-mouth distance (EM), eye diameter (ED), head length (HL), head height (HH), pre-anal length (PreAL), notochord length (NL), body height (BH), yolk length (YL), and yolk height (YH).

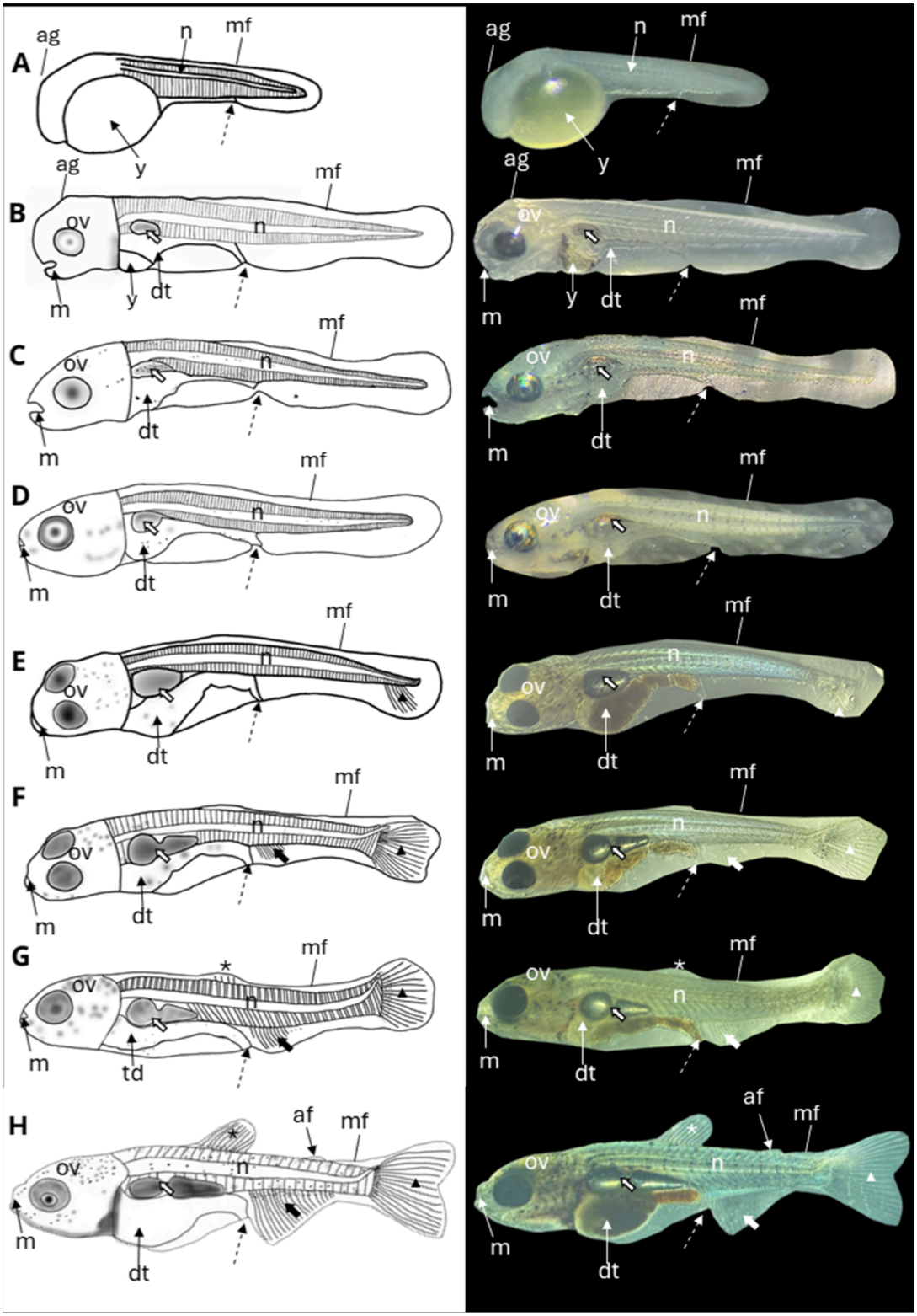


Figure 2

Morphological characteristics of *Moenkhausia oligolepis* larvae during early developmental stages: (A) and (B) yolk-sac larva; (C) and (D) pre-flexion; (E) and (F) flexion; (G) and (H) post-flexion. (A) and (B): ag – adhesive gland; y – yolk; no – notochord; dashed arrow – anal pore; mf – membranous fin; ov – optic vesicle; m – mouth; dt – digestive tract; open arrow – swim bladder. (C) and (D): ov – optic vesicle; m – mouth; no – notochord; dashed arrow – anal pore; dt – digestive tract; mf – membranous fin; open arrow – swim bladder; arrowhead – caudal rays. (E) and (F): ov – optic vesicle; m – mouth; no – notochord; dashed arrow – anal pore; dt – digestive tract; mf – membranous fin; open arrow – swim bladder; arrowhead – caudal rays; thick arrow – anal rays. (G) and (H): ov – optic vesicle; m – mouth; no – notochord; dashed arrow – anal pore; dt – digestive tract; mf – membranous fin; open arrow – swim bladder; arrowhead – caudal rays; thick arrow – anal rays; asterisk – dorsal rays; af – adipose fin.

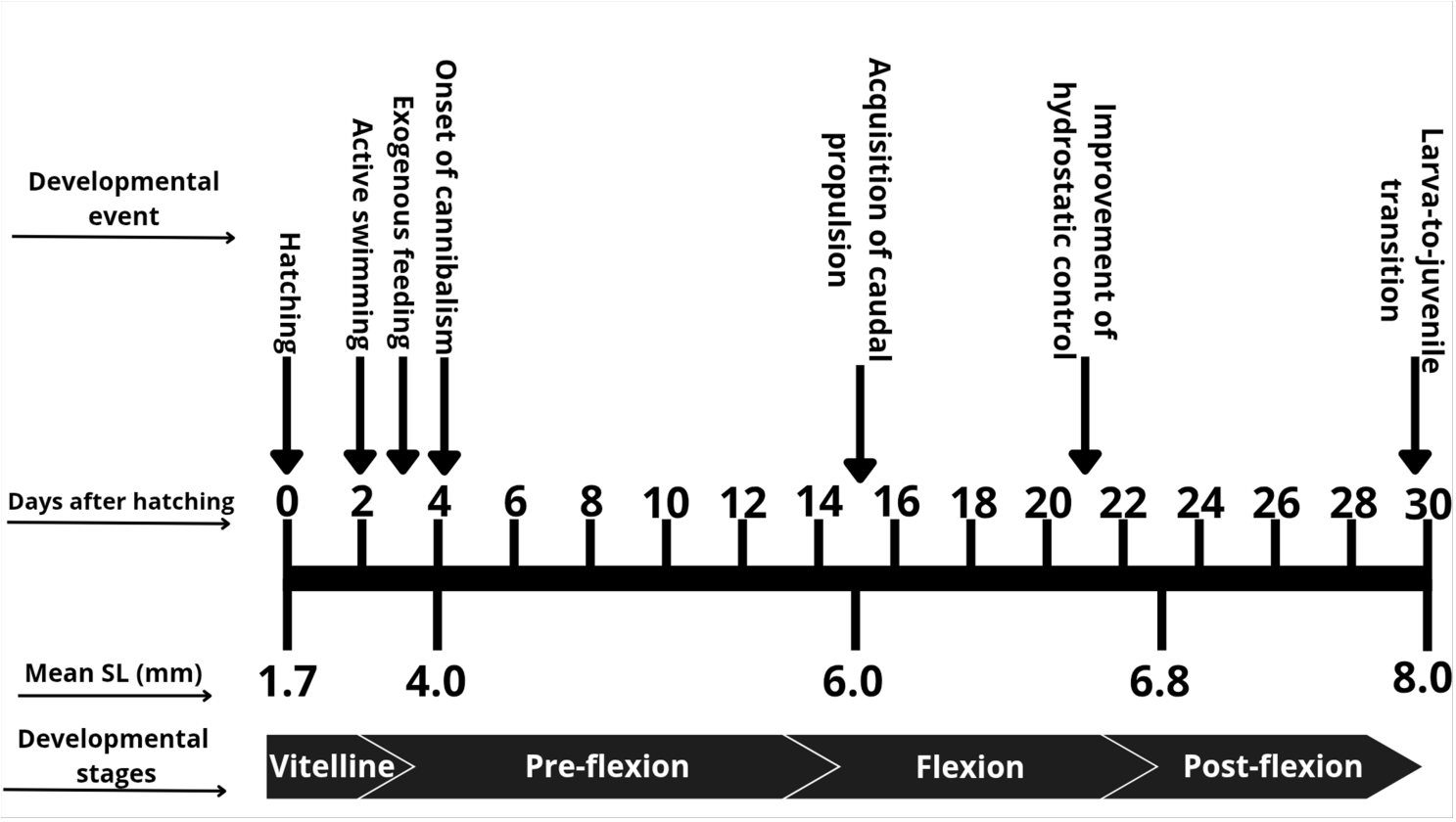


Figure 3

Main developmental events of *Moenkhausia oligolepis* during the larval stages. CP: Standard length; mm: millimeters.

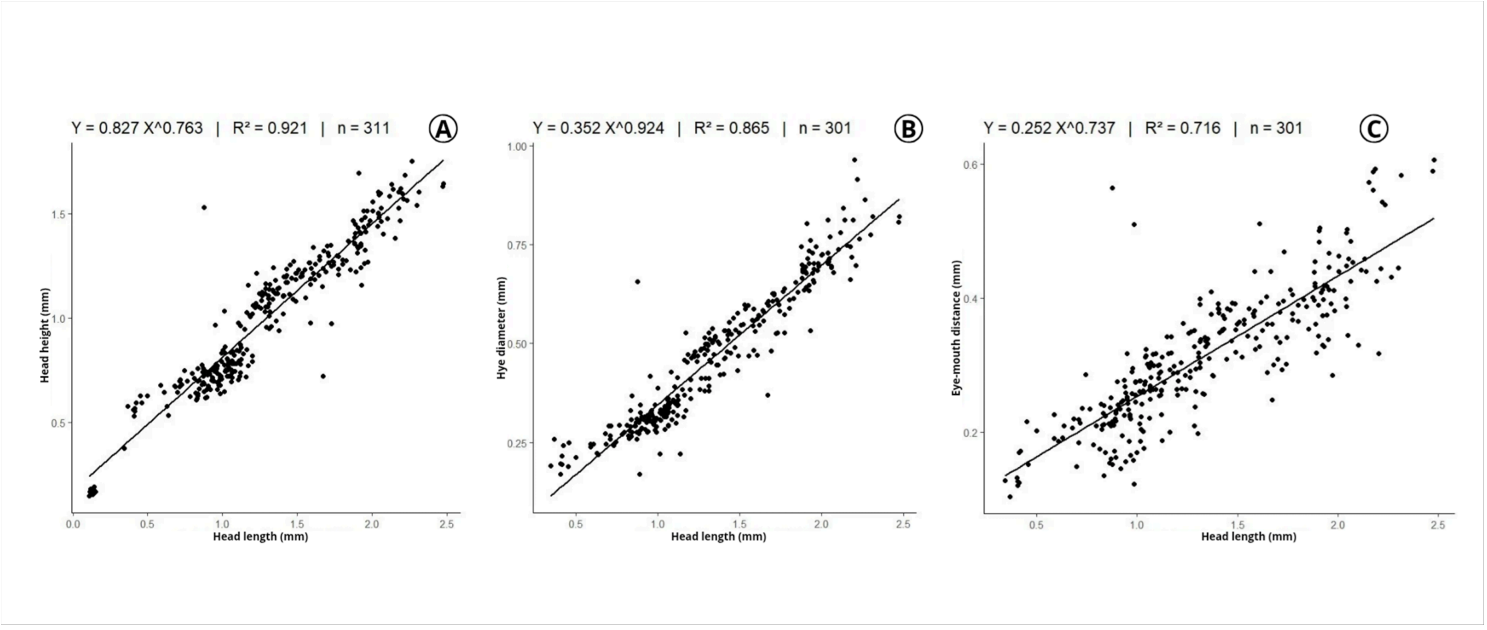


Figure 4

Body proportions of *Moenkhausia oligolepis* obtained as a function of head length: A - head height, B - eye diameter, and C - eye-to-mouth distance. Millimeters (mm).

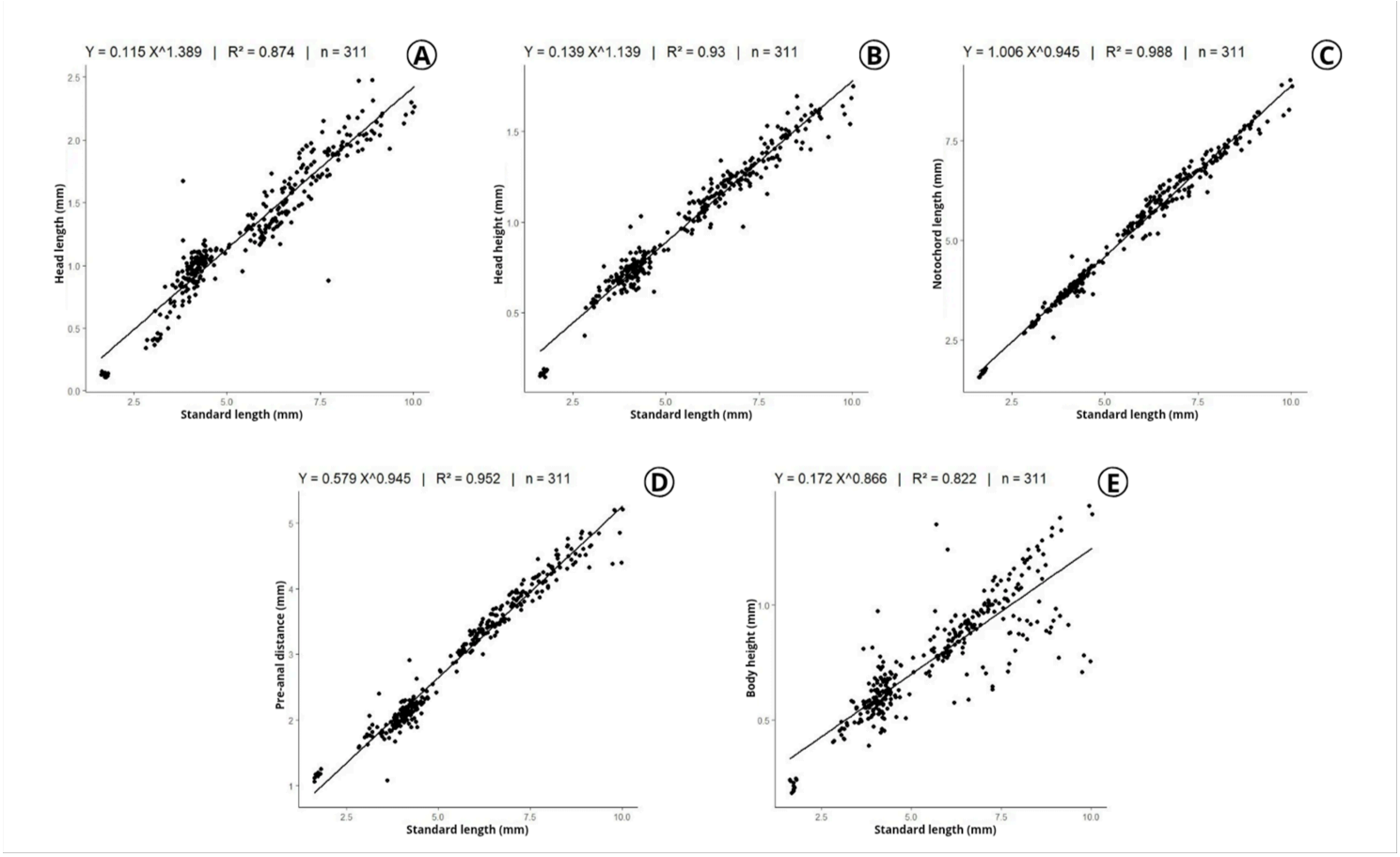


Figure 5

Body proportions of *Moenkhausia oligolepis* obtained as a function of standard length: A - head length; B - head height; C - notochord length; D - preanal distance; and E - body height. Millimeters (mm).

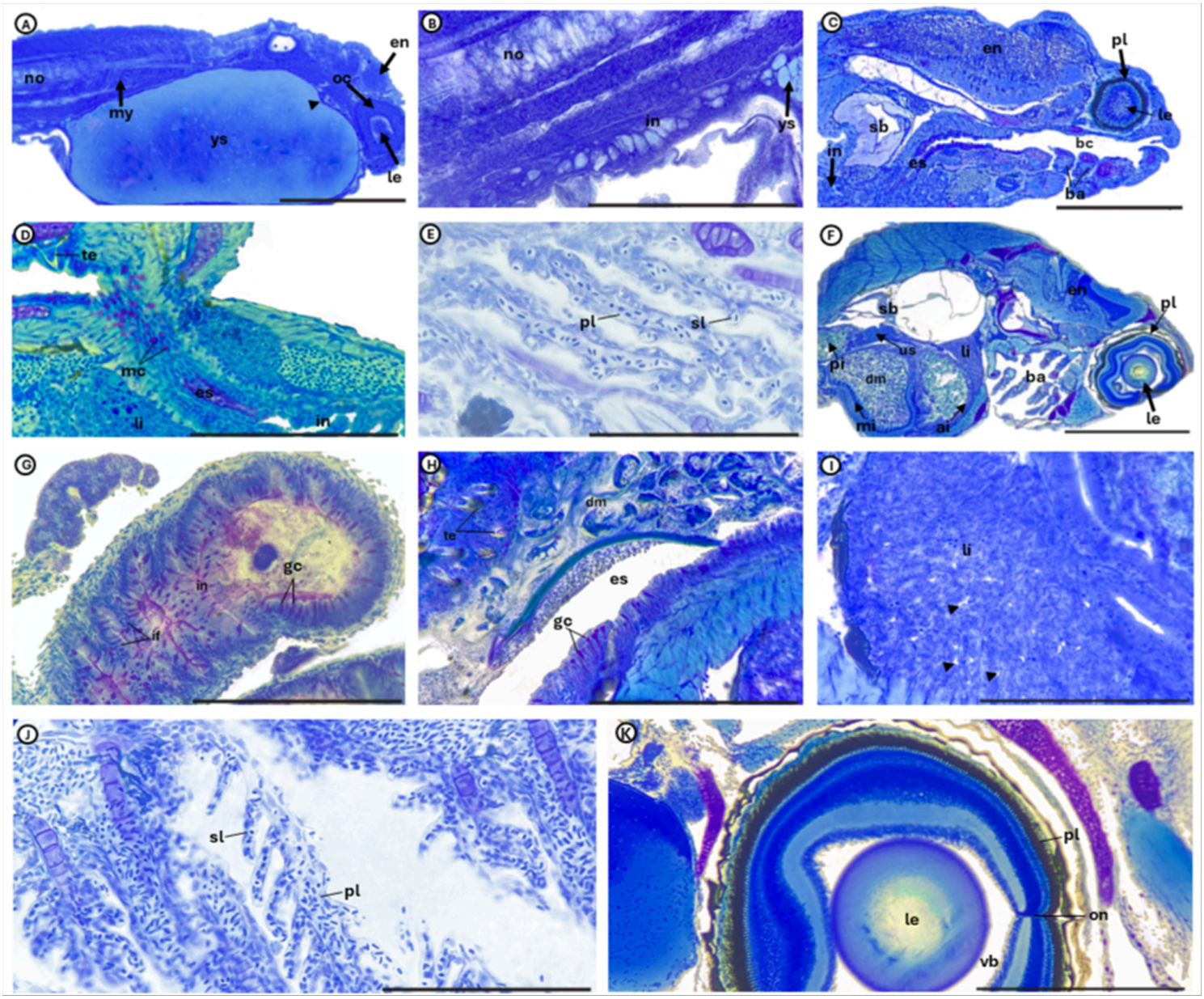


Figure 6

Histological analyses of *Moenkhausia oligolepis* larvae. (A) and (B) 0 DAH: arrowhead – developing heart; ys – yolk sac; my – myomeres; en – encephalon; no – notochord; oc – optic cup; le – lens. (C) and (D) 3 DAH: pl – pigmented layer; le – lens; bc – buccopharyngeal cavity; ba – branchial arches; sb – swim bladder; en – encephalon; es – esophagus; in – intestine; li – liver; mc – mucous cells; te – teeth. (E) 4 DAH (gills): pl – primary lamella; sl – secondary lamella. (F), (G), (H), (I), (J), and (K) 23 DAH: ba – branchial arches; pl – primary lamella; sl – secondary lamella; en – encephalon; sb – swim bladder; us – urinary system; in – intestine; if – intestinal folds; li – liver; pl – pigmented layer; le – lens; dm – digested material; gc – goblet cells; de – teeth; ai – anterior intestine; mi – mid intestine; pi – posterior intestine; arrowhead – hepatic vacuolization; on – optic nerve; vb – vitreous body. Staining: toluidine blue. Scale bars: A, C, and F = 100 µm; B, D, E, and G–K = 50 µm.

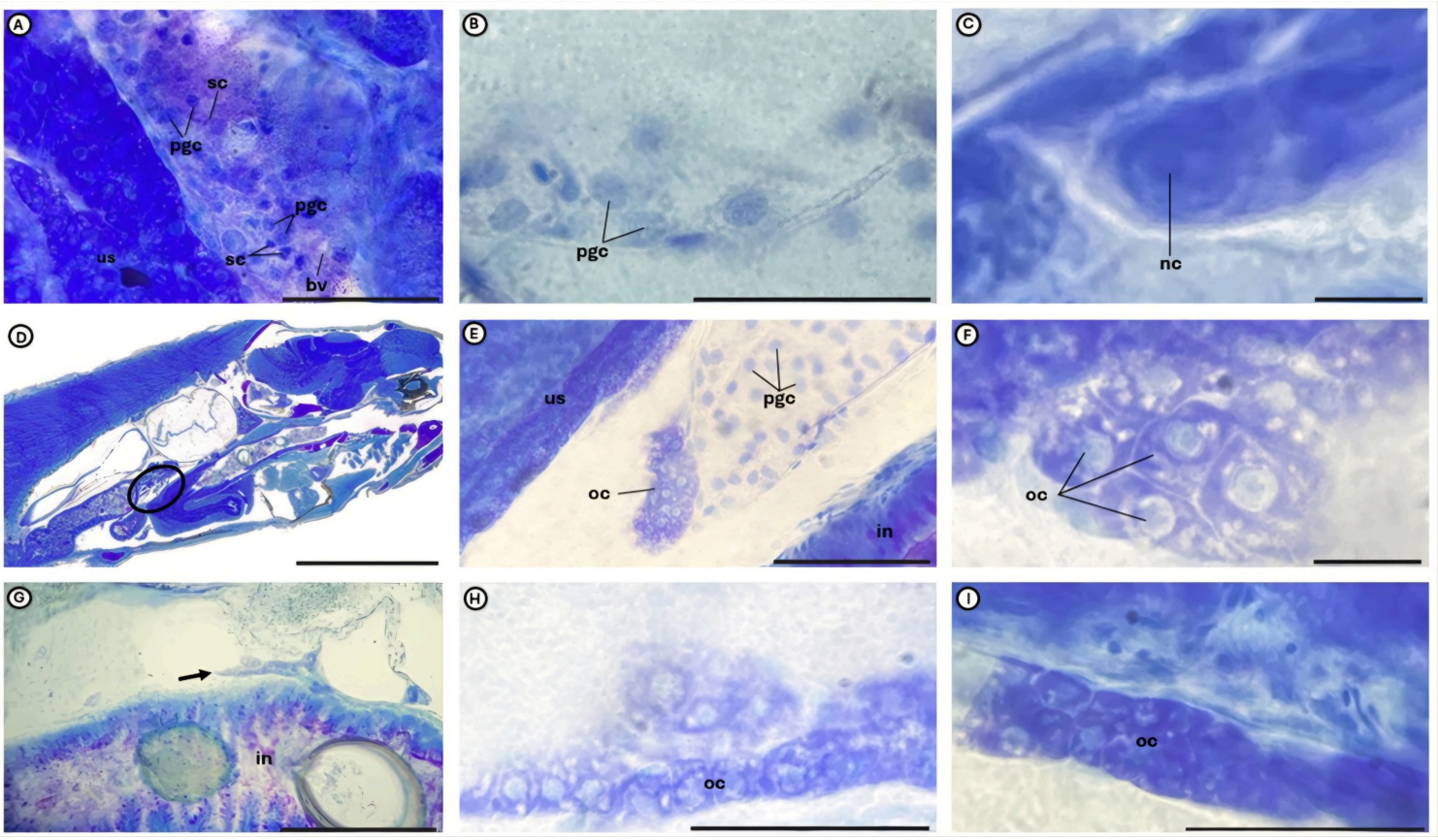


Figure 7

Gonadal differentiation in juveniles of *Moenkhausia oligolepis*. (A) Undifferentiated gonad of a post-larva at 50 days after hatching. (B) Gonadal cord. (C) Detail of a primordial germ cell (PGC). (D), (E), and (G) Location of the female gonads in juveniles. (F), (H), and (I) Organization of the oocytes. PGC – primordial germ cells; sc – somatic cell; bv – blood vessels; us – urinary system; nu – nucleolus; circle – location of oocytes; oc – oocytes; in – intestine; black arrow – indicating oocytes. Staining: toluidine blue. Scale bars: (A), (B), (H), and (I) = 50 µm; (C) and (F) = 20 µm; (D), (E), and (G) = 100 µm.