

Ontogenetic Development Related to Parental Care of a Neotropical Fish, *Pterygoplichthys ambrosettii* (Siluriformes: Loricariidae)

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Received 18 May 2020 / Accepted 17 September 2020 / Published 16 November 2020
Communicated by Felipe Ottoni

This study describes the main ontogenetic changes in the armored catfish *Pterygoplichthys ambrosettii* from newly hatched larva to adult. The relationship between the degree of development of newly hatched larvae and post-larvae and parental care is discussed. Ontogenetic series containing newly hatched larvae, post-larvae, and juveniles of *P. ambrosettii* were obtained from the Fish Culture Station of Universidade Estadual Paulista. Adult specimens were collected from the Preto River in the upper Paraná River basin. Morphological, osteological, morphometric, and meristic data and color pattern were analyzed. The species exhibited indirect development, with a distinct post-larval stage after the larval stage. Newly hatched larvae had a well-developed yolk sac and lacked pigmentation. The following characters underwent less change during development and can therefore be useful in taxonomical analyses: odontodes located posteriorly to the preopercle, number of plates on the lateral line, lower lip with three series of papillae, spots on the upper ray of the caudal fin, caudal fin similar to that of the adult, body ventrally covered with dermal plates and odontodes, small irregular spots on head, and typical ventral color pattern of the adult. The morphometric data revealed that most variation in body proportions occurred during less advanced developmental stages. Parental care influenced the ontogenetic development of newly hatched larvae.

Key words: Armored catfish, Behavior, Larval development, Morphology, Neotropics.

BACKGROUND

Abrupt changes in shape and structure occur during the postembryonic development of fishes. Besides morphological changes, the alterations in physiology, behavior, and ecology are essential to the process of speciation (Honji et al. 2012). The Neotropical region has the largest diversity of fishes in the world (Toussaint et al. 2016), but little is known regarding the early development of species in this region (Lopes et al. 2015).

Among Siluriformes, Loricariidae (armored catfishes) is one of the largest families of Neotropical

freshwater fishes, with about 1000 valid species distributed from Costa Rica in Central America to the La Plata basin in the southern portion of South America (Eschmeyer and Fong 2020). Siluriformes of the genus *Pterygoplichthys* have global-wide distribution through invasion from human aquarium trades (Orfinger and Goodding 2018). Information on the ontogenetic development of loricariids is restricted to knowledge on the developmental stages of a few genera (Machado-Allison and López-Rojas 1975; López-Rojas and Machado-Allison 1975; Garcia-Pinto et al. 1984; Secutti and Trajano 2009). However, the studies cited are based on specimens from the natural environment, where it is

not always possible to obtain an adequate series from the larval to adult stages. The description of ontogenetic transformations is essential to the understanding of the functional trends and environmental preferences of different developmental stages (Honji et al. 2012) and can furnish valuable taxonomic information.

The armored catfish *Pterygoplichthys ambrosettii* (Holmberg, 1893), previously denominated as *Liposarcus anisitsi* (Eigenmann and Kennedy, 1903), which is currently considered a junior synonym of *P. ambrosettii*, is a large loriciid (total length: 50 cm) commonly found in the Turvo River basin in the northwestern region of the state of São Paulo, Brazil (Araujo et al. 2010). Studies on *P. ambrosettii* are restricted to cytogenetics (Artoni et al. 1999), lateral migration (Garutti and Figueiredo-Garutti 2000), microscopic aspects of the accessory air-breathing organ (Oliveira et al. 2001), the purification and crystallization of hemoglobin (Delatorre et al. 2001), and parental care behavior (Cruz and Langeani 2000).

According to Blumer (1982), parental care occurs in 89 families of bony fishes, including the family Loricariidae. Studies on the relation between parental care and the degree of ontogenetic development exhibited by newly hatched loriciid larvae are scarce. The only exception is the study by Garcia-Pinto et al. (1984), who analyzed the reproductive biology of *Hypostomus watwata* from Maracaibo Lake in Venezuela. Therefore, the aims of this work were to 1) describe and analyze the main ontogenetic changes in *P. ambrosettii*, focusing on morphology, color pattern, morphometrics, and meristics from the newly hatched larva to the adult and 2) investigate the possible relationship between ontogenetic development and parental care in this loriciid.

MATERIALS AND METHODS

Ontogenetic series containing newly hatched larvae, post-larvae, and juveniles of *Pterygoplichthys ambrosettii* were obtained from the Fish Culture Station of Universidade Estadual Paulista (UNESP), São José do Rio Preto campus, state of São Paulo, Brazil. Newly hatched larvae, post-larvae, and juveniles were captured directly in the nests or among the aquatic macrophytes (*Heteranthera* sp., Pontederiaceae). Adult specimens were collected from the Preto River (Turvo River system in the upper Paraná River basin) in the municipality of Mirassolândia, state of São Paulo, Brazil (20°32'S 49°29'W). The specimens were fixed in a 10% formaldehyde solution for 48 hours and transferred to a 70° GL ethanol solution for permanent storage. Voucher specimens were deposited in the fish collection of the

Department of Zoology and Botany, UNESP, São José do Rio Preto campus (DZSJRP 2239, 2240, 3749 3750, 3785, 3786, 3791-3793, 3802-3806, 3832-3835, 3837-3842, 3846-3850, 5189-5215, 9296).

The terminology used when describing developmental stages can be confusing due to the variety of terms used by different authors. In this study, the nomenclature follows Hubbs (1943).

Morphology, osteology, and color pattern are expressed based on standard length (SL) measured with calipers. Osteological characters were examined in newly hatched larvae and post-larvae, which were cleared using the method described by Potthoff (1984).

The color pattern was described immediately after fixation to avoid changes in the coloration. Considering the degree of formation and visibility of the structures measured during each stage of development, the following morphometric characters were analyzed.

Newly hatched larvae: i) Total length: measured from snout tip to tip of the most elongated ray of the caudal fin; ii) standard length: distance between snout tip and base of the caudal fin; iii) yolk sac length: distance between origin and end of the yolk sac; iv) eye diameter: measured horizontally, excluding the membrane. Proportions were calculated as ratios of total and standard lengths.

Post-larvae: i) Total length; ii) standard length; iii) predorsal length: distance between snout tip and last pair of predorsal plates; iv) snout length: distance between snout tip and anterior margin of the orbital region, excluding the membrane; v) eye diameter; vi) interorbital width: distance between upper edges of orbital regions; vii) thoracic length: distance between origins of pectoral spine and pelvic spine; pectoral fin spine length, measured from the articulation point of the spine to its tip; viii) abdominal length: distance between origins of pelvic fin spine and anal fin spine; ix) pelvic fin spine length: distance between origin of pelvic fin spine and its tip; x) caudal peduncle length: distance between end of the anal fin and base of the caudal fin. Proportions were calculated as ratios of standard and predorsal lengths.

Juveniles and adults: Characters follow Weber (1992). Proportions were calculated as ratios of standard length, except for parts of the head, which were calculated as ratios of head length (HL).

Unbranched rays of the dorsal, anal, pectoral, pelvic, and caudal fins are indicated by Roman numerals and branched rays are indicated by Arabic numerals. Other counts performed: number of vertebrae including those that originate the Weberian apparatus, except for the urostyle; number of myomeres between anterior and last myoseptum; number of teeth in the premaxillary and dentary bones on both sides; number of dermal

plates between i) first free post-dorsal plate and adipose fin, ii) first free post-adipose plate and penultimate azygous plate on upper caudal fin ray, iii) first post-anal plate and penultimate azygous plate on lower caudal fin ray; number of plates along the lateral line from the first plate anterior to the postcephalic pore to last plate anterior to the lanceolate plates on the median caudal fin rays.

Differences in the mean values of body proportions between the juvenile and adult stages were compared using the Student's t-test for two independent samples (Sokal and Rohlf 2012). Comparisons among post-larval, juvenile, and adult stages were performed using the Kruskal-Wallis test for body proportions followed by the Mann-Whitney multiple comparisons test with a 5% significance level (Zar 1999). All analyses were performed with the aid of the Minitab Statistical Software (1998).

RESULTS

The number and size range of the specimens included eight newly hatched larvae (6.9–8.8 mm), 23 post-larvae (11.3–38.0 mm), 22 juveniles

(53.8–143.3 mm), and 29 adults (200.0–348.0 mm). The cleared individuals were three newly hatched larvae (7.2–9.4 mm) and 15 post-larvae (11.3–38.0 mm).

Morphology

Body

Newly hatched larvae with well-developed, yellowish yolk sac (Fig. 1a) and no visible myomeres or myosepts. Post-larvae with completely absorbed yolk sac (Fig. 1b) and visible myomeres and myosepts; in cleared specimens without yolk sac (from 11.6 mm), functional digestive system is identified, initially in tube form and subsequently in spiral form. Juveniles with rounded anterior profile, which becomes gradually concave anterior to the supraoccipital process; body with slight predorsal elevation and four series of well-developed longitudinal keels (Fig. 2a). Adults exhibit slight predorsal elevation and well-developed longitudinal keels (Fig. 2b); dorsal profile slightly convex and ascending from snout tip to origin of dorsal fin, descending to adipose fin origin, subsequently ascending and following upper caudal profile; ventral profile is approximately straight.



Fig. 1. (a) Lateral view of newly hatched larva of armored catfish *Pterygoplichthys ambrosettii*, DZSJRP 5196, 8.4 mm SL, showing well-developed yolk sac; (b) post-larva, DZSJRP 5191, 11.7 mm SL. Note yolk sac completely absorbed and dorso-lateral pigmentation.

Head

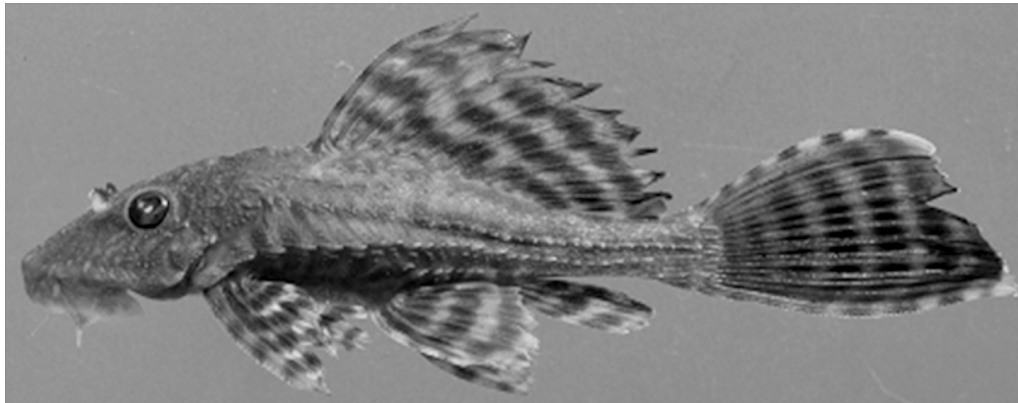
Newly hatched larvae without papillae in lower lip, with one pair of well-developed maxillary barbels almost reaching vertical through anterior orbital margin. Post-larvae with some odontodes on preopercle posterior region. Barbels almost reaching anterior orbital margin. From 32.5 mm, lower lip with papillae in three different regions: first near series of dentary teeth with papillae close to each other and arranged in two series; second with papillae with same size of those of first region but well separated from each other; and third with smaller, more numerous and less separated papillae. Juvenile head with no keels or ridges. Barbels almost reaching end of nostrils in specimens with 53.8 mm. Lower lip with papillae in three distinct regions similar to those found in post-larvae with 32.5 mm. Adult head approximately semielliptical in dorsal view; rounded anterior profile becoming gradually concave anterior to supraoccipital process. Head plates lacking keels or conspicuous ridges. Eye limited by supraorbital margin in contact with pterotic-supracleithrum. Supraoccipital

process flat; posterior region of preopercle often with some odontodes in larger specimens. Ventral suction mouth, large lower lip with papillae in three distinct regions similar to those observed in juveniles with 53.8 mm. Maxillary barbels well developed.

Plates

Newly hatched larvae characterized by absence of dermal plates and associated odontodes. Post-larvae present plates with associated odontodes laterally on posterior region of caudal peduncle, developing from posterior to anterior region of body. From 12.5 to 14.9 mm, specimens have plates with conspicuous odontodes arranged in four longitudinal rows (dorsal, mid-dorsal, median, and mid-ventral), lower most (mid-ventral) reaching tip of pelvic fin and upper restricted to end of caudal peduncle. With 16.1 mm, plates and odontodes appear (i) on posterior region of plate, which will become pterotic-supracleithrum and (ii) from caudal peduncle to body anteriorly and gradually from last to first row. With 17.0 mm, two keels begin at supraorbital

(a)



(b)

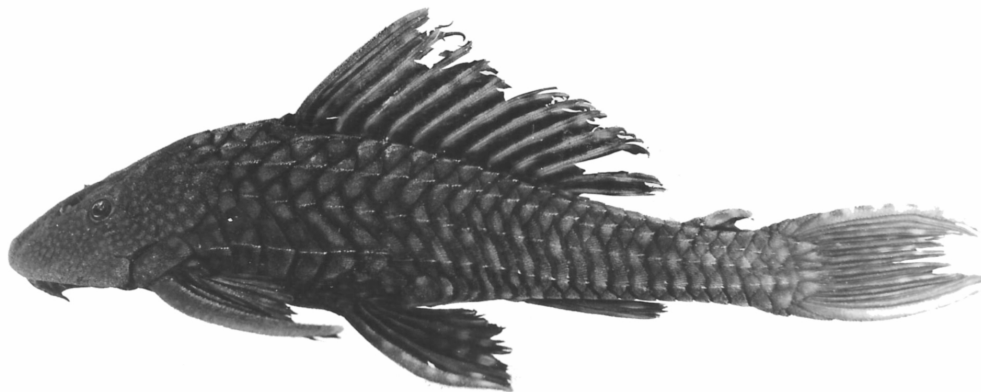


Fig. 2. (a) Lateral view of juvenile of *Pterygoplichthys ambrosettii*, DZSJRP 9296, 53.8 mm SL. Note light brown background color on dorsolateral surface, body with slight predorsal elevation and series of well-developed longitudinal keels; (b) adult, DZSJRP 3837, 212 mm SL. Note dark gray background color and body plates with well-developed odontodes and keels.

margins, extending almost to and converging at level of dorsal-fin spine. From 18.0 mm, post-larvae have four longitudinal series of lateral keels, first (dorsal) and third (median) interrupted in middle of distance between pterotic-supracleithrum and caudal fin, second (mid-dorsal) and fourth (mid-ventral) are complete; with 25.5 mm, only first is incomplete, keels missing on four plates almost in middle of dorsal fin; from 32.5 mm, (i) four complete series, (ii) body covered with plates and odontodes dorso-laterally, and (iii) no plates ventrally between posterior margin of lower lip and beginning of anal fin. Juveniles exhibit odontodes on all fin rays, more numerous and conspicuous on unbranched rays. From 73.4 mm, ventrally, only region between posterior margin of lower lip and pectoral girdle not covered with plates and odontodes. Abdomen fully plated when reaching 114.8 mm. Adults have body plates with well-developed odontodes and keels. Dorsum and laterals with weakly striated plates. On each plate, one median row of enlarged odontodes forms ridges aligned in four series of lateral keels on each side of body up to lanceolate plates of caudal fin. Upper keel near dorsal fin begins in first plate posterior to occipital process/pterotic-supracleithrum junction; mid-dorsal keel originates in upper portion of first plate posterior to pterotic-supracleithrum; median keel begins on second plate (third plate in one specimen) posterior to edge of pterotic-supracleithrum; mid-ventral keel begins on posterior plate of cleithrum. Abdomen is covered with small plates, with no visible preanal plate.

Fins

Newly hatched larvae exhibit emergent pectoral and pelvic fins, less developed pelvic fins, caudal fin completely formed and rounded, dorsal and anal fins in advanced stage of development, and absence of adipose fin. Post-larvae exhibit all formed fins and emarginate caudal fin. Juveniles from 53.8 mm exhibit caudal fin with elongated unbranched rays, lower spine longer than upper. Adults have odontodes on all fin rays, more numerous and conspicuous on unbranched rays. Pectoral fin reaches posteriorly to end of pelvic fin when adpressed to body and exhibits dorso-ventrally flattened spine with inconspicuous odontodes on distal portion. Pelvic fin extends to anal fin base. Adipose fin well-developed, with larger and curved spine. Caudal fin similar to that in juvenile specimens.

Osteology

Newly hatched larvae dorsally exhibit (i) cranium bones with larger spaces among sutures, (ii) five pairs of gill arches without filaments, and (iii) absence of otic

capsule and parapophyses. Pectoral and pelvic girdles are incomplete. Dorsal, anal, caudal, and pectoral fins are almost completely ossified and pelvic fins are poorly developed. Vertebrae and hypural complex are completely formed and ossified. Body completely colored Alcian blue, mainly on barbels and base of all fin rays, indicates the absence of ossification. Post-larvae show (i) cranium bones with sutures well stained by Alcian blue when in dorsal view, (ii) five pairs of gill arches with filaments, and (iii) otic capsule and parapophyses in development. The first girdle formed is pectoral; pelvic is complete when post-larvae reach approximately 12.3 mm. At this size, (i) two series of upper lateral keels appear with single odontodes and two lower series appear with double odontodes, (ii) pectoral, pelvic, anal, and caudal-fin spines with few odontodes, (iii) dorsal spine with large quantity of odontodes, and (iv) epural rays with numerous odontodes. With 12.7 mm, cleithrum is stained by Alizarin (first bone in this stage in which cartilaginous tissue is replaced by bone tissue) and odontodes noted in region of otic capsule. From 13.3 mm, post-larvae have spines and odontodes at end of caudal peduncle stained red by Alizarin. From 16.9 to 21.0 mm, base of dorsal, anal, pectoral, and pelvic fin rays is stained by Alcian blue, except for base of the dorsal and pectoral fin spines, which are stained by Alizarin. When reaching 30.6 mm, caudal fin exhibits distal portion of urostyle stained blue. From 32.5 to 38.0 mm, urostyle is completely ossified. Vertebral column becomes reddish from 16.9 mm. With 24.6 mm, only first and fourth series of lateral keels are incomplete. From 30.6 mm, fourth series is formed. Cranium bones, such as lateral ethmoid (distal portion), metapterygoid (base), supraorbital, and suture between frontal and supraoccipital process are stained blue from 16.9 to 25.1 mm. With 32.5 mm, sutures between frontal, supraoccipital, and pterotic-supracleithrum bones are conspicuous. Cranium floor exhibits cartilages resembling trabecular bars and parachordal plates stained blue when reaching 38.0 mm.

Color pattern

In the post-larval and juvenile stages, the color pattern on all fins is transverse dark brown bands, except on the dorsal fin, which has longitudinal bands.

Newly hatched larvae only exhibit some pigment between nostrils and snout, forming two inconspicuous bands in the region of the occipital process and the base of the caudal fin. Post-larvae exhibit laterally pigmented yellow yolk sac, more uniform brown dorso-lateral pigmentation with three clusters of brown dots alternating with unpigmented areas in the region of nostril, which will originate three longitudinal bands.

Areas anterior to the adipose fin as well as spines of dorsal and caudal fins are unpigmented. At 11.5 mm, all fins are unpigmented, except the caudal fin, which has dark gray base. From 12.5 mm, pigment appears on pectoral, anal, pelvic, and caudal fins. In the median and terminal regions of the caudal fin, clusters of dark pigments appear followed by brown band and subsequently sparse dark pigments. With 13.7 mm, two dark spots on both spines and one brown band in terminal portion. With 23.9 mm, four black bands alternating with light brown bands. Specimens with 25.5 mm exhibit black background color. With 32.5 mm, four dark spots on upper caudal ray alternate with transparent and brown areas. With 38.0 mm, five transverse black bands are observed. With 18.0 mm, the dorsal fin exhibits two inconspicuous bands, increasing to three (with 19.6 mm) and four (with 23.9 mm) dark brown bands, which alternate with brown spots when reaching 25.5 mm. With 32.5 mm, spine exhibits five brown spots. Ventrally, post-larvae with 38.0 mm exhibit yellowish color, with some brown pigments appearing when reaching 32.5 mm.

Juveniles with 53.8 mm have light brown background color on dorsolateral surface. Ventrally, small irregular light spots appear in region between pelvic and pectoral girdles. When reaching 73.4 mm, the head exhibits (i) small irregular brown spots (conspicuous on pterotic-supracleithrum), (ii) ventrally, small slight spots slightly rounded that become larger and irregular from pectoral girdle to pelvic girdle, which increase in size, and (iii) black and brown spots dorsally. From 80.4 mm, brown spots disappear. With 94.9 mm, dark brown spots are noted. Dorsum becomes uniformly dark gray when reaching 114.8 mm. Generally, spots on fin spines increase in quantity until specimens reach 126.2 mm, except for upper caudal-fin ray, which exhibits spots in adult specimens, with completely pigmented spines. Dorsal, anal, and pelvic fins exhibit two black bands alternating with transparent and/or light brown areas when the specimens reach 53.8 mm; with 83.6 mm, dark brown color replaces light brown and number of bands increases. Pectoral fin initially has three black bands alternating with transparent (interradial membranes) and light brown (rays) areas, which become black when reaching 83.6 mm. With three irregular black bands, caudal fin alternates light and brown color areas (60.5 mm) and dark gray (four to five bands from 73.6 to 126.2 mm).

Adults have dark gray background color, more intense dorsally than ventrally. Head with small irregular light spots without vermiculations; in some specimens, spots are more conspicuous on pterotic-supracleithrum than remaining parts of head. Dorsum is uniformly grayish without vermiculations. Ventrally,

head is characterized by small light slightly rounded spots that become larger and irregular from pectoral girdle to pelvic girdle, which increase in size and enlarge in some cases; in region between pelvic and anal fins, spots can be reduced to uncolored marks or reducing in quantity; in this case, dark background color is predominant on spots. Unbranched rays of pectoral and adipose fins exhibit light spots; anal spine has no spots. Branched rays of anal and caudal fins exhibit light spots distally; pelvic fin exhibits spots in median portion, sometimes distally; other fins often with spots poorly defined. Upper caudal fin ray exhibits irregular light spots. Interradial membranes darkish, except for unpigmented specimens.

Morphometrics

Tables 1 to 3 show morphometric data for newly hatched larvae, post-larvae, juveniles, and adults of *P. ambrosettii*. The Student's t-test revealed significant differences ($p < 0.05$ or $p < 0.001$) between the juvenile and adult stages for all body proportions, except caudal-peduncle depth/SL, and interorbital width/HL (Table 4). The Kruskal-Wallis test revealed significant differences ($p < 0.001$) for all body proportions among post-larval, juvenile, and adult stages (Table 5). The Mann-Whitney test revealed significant differences ($p < 0.001$) between post-larvae and juveniles as well as between post-larvae and adults for all body proportions, whereas no significant differences between juveniles and adults were found for thoracic length/SL, pectoral-spine length/SL, and abdominal length/SL (Table 5).

Meristics

The main ontogenetic changes were the number of teeth [premaxillary: 6–19 (post-larvae), 11–33 (juveniles), 19–37 (adults); dentary: 7–21 (post-larvae), 14–34 (juveniles), 18–38 (adults)] and plates [dorsal to adipose: 6 (juveniles), 6–7 (adults); adipose to caudal: 4–5 (juveniles), 5–7 (adults); anal to caudal: 10–13 (juveniles), 13–16 (adults)] (Table 6).

DISCUSSION

Analyzing development and phylogenetics in Ostariophysi, Fuiman (1984) states that the size at hatching of Siluriformes ranges in total length (TL) from 3 to 8 mm. According to different studies, the size of Loricariidae at hatching is broader than this range, with a mean of 3.2 mm (SL) for *Rhinelepis strigosa* (Nakatani et al. 2001), 5.6 mm (SL) for *Ancistrus* cf. *triradiatus* (Geerinckx et al. 2007), 9.1 mm (SL) for

Ancistrus cryptophthalmus (Secutti and Trajano 2009), 10.14 mm (TL) for *Hypostomus watwata* (Garcia-Pinto et al. 1984), 8.42 mm (SL) for *Loricariichthys typus* (Machado-Allison and López-Rojas 1975), 12 mm (TL) for *Loricaria uracantha* (Moodie and Power 1982), and 15.99 mm (SL) for *Loricaria laticeps* (López-Rojas and Machado-Allison 1975). In the present study, mean TL at hatching was 9.6 mm for *Pterygoplichthys ambrosettii*.

In this study, no variation was found in the number of vertebrae or rays on the dorsal, anal, and caudal fins between the larval and post-larval stages. According to Ochoa et al. (2010), meristic characteristics, such as vertebrae and myomere number, are considered good tools for the taxonomic identification of fish species at different stages of development.

Studying the development and fine structure of bony plates in *Corydoras arcuatus* (Callichthyidae),

Sire (1993) found that the first dermal plates appear in the posterior region of the caudal peduncle in specimens from 11.5 to 15.0 mm SL, subsequently moving toward the anterior region of the body. Describing developmental stages in *Hoplosternum littorale* (Callichthyidae), Machado-Allison (1986) found that the ossification of dermal plates in specimens with 18.5 mm TL begins in the caudal region, subsequently moving toward the anterior region of the body. Both regions where plates appear and the direction of the development in *H. littorale* are in agreement with what was found in *P. ambrosettii* post-larvae when reaching 11.5 mm SL.

Juveniles are distinguished from post-larvae by having a body with dermal plates covered by odontodes ventrally, a color pattern with a dark gray background color that is more intense dorsally than ventrally, and larger number of premaxillary and dentary teeth. The

Table 1. Morphometric data (mm) for newly hatched larvae and post-larvae of the armored catfish *Pterygoplichthys ambrosettii*

Character	n	Mean	SD	Range
Newly hatched larvae				
Total length	8	9.6	0.82	8.5–10.8
Standard length	8	7.9	0.61	6.9–8.8
Yolk sac length	8	3.8	0.51	3.2–4.9
Eye diameter	8	0.5	0.07	0.3–0.5
Standard length/TL	8	1.2	0.03	1.2–1.3
Yolk sac length/TL	8	2.6	0.46	1.7–3.3
Yolk sac length/SL	8	2.1	0.37	1.4–2.6
Eye diameter/SL	8	17.3	2.46	15.6–23.0
Post-larvae				
Total length	22	26.3	10.55	15.9–53.9
Standard length	22	19.3	7.40	12.1–38.0
Predorsal length	22	8.5	3.51	5.1–18.1
Thoracic length	22	3.6	1.82	1.6–7.9
Pectoral spine length	22	4.3	2.53	1.7–10.6
Abdominal length	22	2.8	1.64	1.4–7.2
Pelvic spine length	22	3.7	2.08	1.4–8.6
Caudal peduncle length	22	4.7	1.96	2.4–9.1
Snout length	22	3.4	1.71	1.4–8.1
Eye diameter	22	1.3	0.53	0.6–2.3
Interorbital width	22	2.6	1.31	1.2–5.9
Predorsal length/SL	22	2.3	0.09	2.1–2.5
Thoracic length/SL	22	5.7	0.93	4.4–7.8
Pectoral spine length/SL	22	5.0	1.02	3.6–7.3
Abdominal length/SL	22	7.5	1.65	5.1–12.1
Pelvic spine length/ SL	22	5.8	1.34	4.3–8.6
Caudal peduncle length/SL	22	4.1	0.36	3.6–5.0
Snout length/PrD	22	2.6	0.39	2.1–3.6
Eye diameter/PrD	22	7.0	1.03	5.1–9.8
Interorbital width/PrD	22	3.4	0.55	2.9–4.9

Body proportions as ratios of total length (TL), standard length (SL), and predorsal length (PrD). n = number of specimens examined, SD = standard deviation.

lack of knowledge on early and juvenile development often makes it difficult to decide when a fish becomes a juvenile. This stage corresponds to the period in which the young are essentially similar to adults, as found in *P. ambrosettii*. The meristic analysis revealed no variation in the number of fin rays between the post-larval and juvenile stages.

As juveniles resemble adults, the identification

of the stage of gonadal development is essential, since it is not always possible to state whether a specimen is a juvenile or adult based on external features. Valdener Garutti (pers. com.) found that *P. ambrosettii* is immature and mature when its gonads are at 180 mm SL and 280 mm SL, respectively. In the present study, the morphometric data demonstrated no changes in body proportions from the juvenile to the adult stages.

Table 2. Morphometric data (mm) for juveniles of the armored catfish *Pterygoplichthys ambrosettii*

Character	n	Mean	SD	Range
Standard length	22	93.4	24.51	53.8–143.3
Axial length	22	116.9	29.67	68.7–175.0
Total length	22	137.6	33.84	78.1–196.0
Predorsal length	22	37.1	9.52	23.8–58.6
Head length	22	31.2	7.22	20.3–46.4
Cleithral width	22	26.5	7.22	16.2–42.3
Head depth	22	18.7	5.14	11.9–31.2
Snout length	22	16.1	4.05	10.2–25.2
Eye diameter	22	4.0	0.61	3.0–5.3
Interorbital width	22	14.2	3.68	8.6–22.3
Dorsal spine length	21	26.8	6.53	14.8–39.6
Dorsal base length	22	34.1	9.61	18.8–54.5
Dorsal-adipose distance	22	12.2	3.52	6.4–19.0
Thoracic length	22	20.7	6.01	11.0–33.5
Pectoral spine length	22	28.3	7.85	15.4–42.0
Abdominal length	22	21.3	6.38	10.9–34.0
Pelvic spine length	22	23.8	6.67	13.2–37.3
Caudal peduncle length	22	27.3	8.37	14.7–47.0
Caudal peduncle depth	22	8.7	2.79	3.9–15.0
Barbel length	22	2.6	1.01	0.7–5.3
Adipose spine length	22	6.6	1.83	3.4–10.5
Upper caudal fin ray	20	36.0	9.30	17.6–51.3
Lower caudal fin ray	22	42.2	9.43	23.4–57.9
Predorsal length/SL	22	2.5	0.11	2.3–2.6
Head length/SL	22	3.0	0.16	2.5–3.1
Cleithral width/SL	22	3.5	0.16	3.3–3.8
Dorsal spine length/SL	21	3.4	0.31	2.9–4.3
Dorsal base length/SL	22	2.7	0.09	2.5–2.9
Dorsal-adipose distance/SL	22	7.8	0.72	6.6–9.4
Thoracic length/SL	22	4.5	0.21	4.2–4.9
Pectoral spine length/SL	22	3.3	0.24	2.8–3.8
Abdominal length/SL	22	4.4	0.26	3.8–5.0
Pelvic spine length/SL	22	3.9	0.31	3.5–4.9
Caudal peduncle length/SL	22	3.5	0.25	2.8–3.8
Caudal peduncle depth/SL	22	11.0	0.96	9.5–13.8
Adipose spine length/SL	22	14.3	2.29	11.6–22.2
Upper caudal fin ray/SL	20	2.6	0.45	2.0–4.0
Lower caudal fin ray/SL	22	2.2	0.32	1.9–3.1
Cleithral width/HL	22	1.2	0.05	1.1–1.3
Head depth/HL	22	1.7	0.09	1.5–1.9
Snout length/HL	22	1.9	0.07	1.8–2.1
Eye diameter/HL	22	7.7	1.24	6.6–12.4
Interorbital width/HL	22	2.2	0.08	2.1–2.4

Body proportions as ratios of standard length (SL) or head length (HL). n = number of specimens examined, SD = standard deviation.

Regarding the counts, the number of teeth, and plates between dorsal and adipose fins, adipose and caudal fins, as well as the anal fin and end of the caudal peduncle increased in adults compared to juveniles.

Characters such as (i) the presence of some odontodes posterior to the preopercle, (ii) number of plates along the lateral line, (iii) lower lip with papillae and spots in the upper caudal fin ray (post-larval stage), (iv) caudal fin similar to that of the adult, (v) whole body covered with dermal plates and odontodes ventrally, (vi) small irregular spots on the head, and

(vii) typical ventral color pattern of adults underwent less changes during ontogenetic development and are therefore useful for taxonomical analyses.

Considering only juvenile and adult stages, the body proportions indicate a high degree of variation in body measurements, except for caudal-peduncle depth/SL and interorbital width/HL, which appear to remain practically stable as the individual grows. However, when comparing post-larval, juvenile, and adult stages, statistically significant differences were found for all body proportions. The considerable variation in these

Table 3. Morphometric data (mm) for adults of armored catfish *Pterygoplichthys ambrosettii*

Character	n	Mean	SD	Range
Standard length	29	285.7	41.84	200.0–348.0
Axial length	29	329.5	48.71	235.0–405.0
Total length	29	351.8	49.07	255.0–425.0
Predorsal length	29	109.6	16.92	76.9–136.6
Head length	29	80.5	11.45	59.0–98.8
Cleithral width	29	72.07	8.61	54.0–85.0
Head depth	29	51.3	7.18	38.2–65.0
Snout length	29	44.6	6.69	32.0–56.7
Eye diameter	29	6.5	0.67	5.0–7.9
Interorbital width	29	36.3	4.94	26.2–44.7
Dorsal spine length	26	66.9	9.22	46.2–86.7
Dorsal base length	29	98.8	15.29	68.6–124.6
Dorsal-adipose length	29	41.0	7.84	26.6–55.3
Thoracic length	29	63.4	9.20	47.2–78.6
Pectoral spine length	29	85.1	10.53	60.8–100.6
Abdominal length	29	65.1	10.69	44.2–82.6
Pelvic spine length	29	65.4	7.98	42.0–78.0
Peduncle caudal length	29	89.5	12.26	64.6–115.8
Peduncle caudal depth	29	26.1	3.77	18.0–32.0
Barbel length	29	10.5	2.61	5.6–15.7
Adipose spine length	29	18.3	2.27	13.0–22.4
Upper caudal fin ray	29	64.5	10.71	39.0–85.6
Lower caudal fin ray	29	64.6	11.48	31.3–86.5
Predorsal length/SL	29	2.6	0.09	2.4–2.8
Thoracic length/SL	29	4.5	0.31	4.0–5.3
Pectoral spine length/SL	29	3.3	0.16	3.1–3.8
Abdominal length/SL	29	4.4	0.14	4.1–4.7
Pelvic spine length/SL	29	4.4	0.27	3.9–5.0
Peduncle caudal length/SL	29	3.2	0.18	2.9–3.8
Peduncle caudal depth/SL	29	10.9	0.51	10.1–12.0
Adipose spine length/SL	29	15.6	1.12	14.2–17.5
Upper caudal fin ray/SL	29	4.5	0.81	3.6–6.5
Lower caudal fin ray/SL	29	4.5	0.92	3.4–7.5
Cleithral width/HL	29	1.1	0.04	1.0–1.2
Head depth/HL	29	1.6	0.06	1.4–1.7
Snout length/HL	29	1.8	0.05	1.7–1.9
Eye diameter/HL	29	12.4	1.18	10.4–15.0
Interorbital width/HL	29	2.2	0.06	2.1–2.4
Adipose spine length	29	18.3	2.27	13.0–22.4
Upper caudal fin ray	29	64.5	10.71	39.0–85.6

Body proportions as ratios of standard length (SL) or head length (HL). n = number of specimens examined, SD = standard deviation.

Table 4. Mean, standard deviation (SD) and results of Student’s t-test for body proportions as ratios of standard length (SL) or head length (HL) between juveniles ($n = 22$) and adults ($n = 29$) of armored catfish *Pterygoplichthys ambrosettii*

Proportion	Mean \pm SD		p
	Juveniles	Adults	
Caudal peduncle depth/SL	11.0 \pm 0.98	10.9 \pm 0.51	0.890 ^{NS}
Adiposespine length/SL	14.3 \pm 2.29	15.6 \pm 1.12	0.017*
Upper caudal fin ray/SL	2.6 \pm 0.45	4.5 \pm 0.81	0.000***
Lower caudal fin ray/SL	2.2 \pm 0.32	4.5 \pm 0.92	0.000***
Cleithral length/HL	1.2 \pm 0.05	1.1 \pm 0.04	0.000***
Head depth/HL	1.7 \pm 0.09	1.6 \pm 0.06	0.000***
Snout length/HL	1.9 \pm 0.07	1.8 \pm 0.05	0.000***
Eye diameter/HL	7.7 \pm 1.24	12.4 \pm 1.18	0.000***
Interorbital width/HL	2.2 \pm 0.08	2.2 \pm 0.06	0.630 ^{NS}

* $p < 0.05$; *** $p < 0.001$; NS = non-significant.

Table 5. Median, H values of Kruskal-Wallis test and Mann-Whitney test of body proportions as ratio of standard length (SL) among 22 post-larvae (PL), 22 juveniles (J), and 29 adults (A) of armored catfish *Pterygoplichthys ambrosettii*

Proportion	Median			H	Mann-Whitney Test		
	PL	J	A		PL \times J	PL \times A	J \times A
Predorsal length/SL	2.3	2.5	2.6	47.01***	***	***	***
Thoracic length/SL	5.6	4.6	4.5	33.47***	***	***	NS
Pectoral spine length/SL	5.3	3.3	3.3	43.56***	***	***	NS
Abdominal length/SL	7.1	4.4	4.4	45.53***	***	***	NS
Pelvic spine length/SL	5.5	3.9	4.3	46.52***	***	***	***
Caudal peduncle length/SL	4.1	3.5	3.2	52.36***	***	***	***

*** $p < 0.001$; NS = non-significant.

Table 6. Meristic data on newly hatched larvae, post-larvae, juveniles, and adults of armored catfish *Pterygoplichthys ambrosettii*. Counts of vertebrae, myomeres, body plates, teeth, and fin rays. Number of specimens examined (n)

Characters	Newly hatched larvae ($n = 8$)	Post-larvae ($n = 23$)	Juveniles ($n = 22$)	Adults ($n = 30$)
Vertebrae	28	28	**	**
Myomeres	*	28	**	**
Lateral line plates	*	28–30	28–30	27–30
Dorsal-adipose plates	*	*	6	6–7
Adipose-caudal plates	*	*	4–5	5–7
Anal-caudal plates	*	*	10–13	13–16
Premaxillary teeth	*	6–19	11–33	19–37
Dentary teeth	*	7–21	14–34	18–38
Dorsal fin rays	i + 12	i + 12	i + 12	i + 12
Anal fin rays	i + 4	i + 4	i + 4	i + 4
Pectoral fin rays	i + 5	i + 6	i + 6	i + 6
Pelvic fin rays	*	i + 5	i + 5	i + 5
Caudal fin rays	8 + 8	8 + 8	8 + 8	8 + 8

* absent or poorly visible; ** not counted.

proportions may be due to the fact that *P. ambrosettii* undergoes very accentuated ontogenetic changes, especially during less advanced developmental stages. These findings can be an extremely valuable tool for taxonomic studies. Considerable morphological similarity among different taxonomic groups has been the main obstacle to identifying larvae collected from the natural environment (Isari et al. 2017). Morphometric analyses enable the different developmental stages to be compared within and between species and, together with other characteristics, permit the correct identification of larvae.

Parental care and ontogenetic development

Members of at least nine Siluriform families exhibit parental care of the young (Breder and Rosen 1966). Ariids carry the eggs in the mouth, whereas aspredinids and loricariids carry the eggs on the body surface (Maciel et al. 2018; Carvalho et al. 2015; Suzuki et al. 2000). Freshwater ariids as well as some doradids, plotsids, silurids, ictalurids, saccobranchids, and callichthyids build nests and/or guard the eggs (Blumer 1982; Andrade and Abe 1997).

According to Fuiman (1984), Siluriformes has the greatest diversity of larval characters within the Ostariophysi. Some families, such as Ictaluridae, exhibit direct development with well-pigmented offspring and a nearly absorbed yolk sac, with appearance and body form essentially equal to those of adults, denoting the absence of a post-larval stage (Mayden et al. 1980; Mayden and Burr 1981). Some loricariids also hatch at an early stage resembling adults, such as *Loricaria laticeps* (López-Rojas and Machado-Allison 1975) and *Ancistrus* cf. *triradiatus* (Geerinckx et al. 2007; Geerinckx et al. 2008). In the present study, *P. ambrosettii* exhibited indirect development, with a distinct post-larval stage after the larval stage. The demarcation of these stages was based on changes occurring mainly in external morphology.

P. ambrosettii constructs nests for spawning and the initial development of the eggs and larvae (Cruz and Langeani 2000). In this species, newly hatched larvae exhibit a very developed yellowish yolk sac as well as the absence of dermal plates and odontodes, as described by Garcia-Pinto et al. (1984) for *Hypostomus watwata* (Hypostominae). Newly hatched larvae of both species are also virtually unpigmented, with only some pigment on the head between the orbits and between the nostrils and snout, forming two inconspicuous bands in the region of the occipital process and base of the caudal fin in *P. ambrosettii*, in which the pectoral and pelvic girdles are incomplete, and the pelvic fin is poorly developed. López-Rojas and Machado-

Allison (1975) studied the development and growth of *Loricaria laticeps* (Loricariinae), in which the egg mass is attached to the ventral surface of body, and found that newly hatched larvae exhibit defined pigmentation in all regions of the body, a series of plates with odontodes, all fins formed, and a poorly absorbed yolk sac. Investigating the developmental stages of *Loricariichthys typus* (Loricariinae), which carries the eggs with the lips, Machado-Allison and López-Rojas (1975) found that post-larvae exhibit a highly developed yolk sac, relatively well pigmented body, and poorly developed series of plates and odontodes, resembling the post-larvae of *P. ambrosettii* at 11.5 mm SL. Therefore, the larvae in of these loricariids hatch in a more advanced stage of development compared to species of Hypostominae. Although the larvae hatch in an earlier stage in *P. ambrosettii*, they remain in the nest for a period, enabling a degree of development (Cruz and Langeani 2000) comparable to that of the family Loricariinae after hatching. These adaptations may ensure a better chance of survival for the larvae. According to Balon (1975), the eggs of species that exhibit some parental care are larger, need more time to hatch, and produce more viable larvae, which increase the survival rate of the offspring. The advanced degree of development may be an ecological advantage for the species, since more developed offspring may be able to exploit more niches and may be less susceptible to predation. Moreover, the pigmentation of the newly hatched larvae favors camouflaging in vegetation, which decreases the risk of being eaten (Araujo and Garutti 2003).

Species that do not construct nests and those with a less developed mechanism for parental care generally have larvae that hatch in a more advanced stage, corresponding to the post-larval stage of *P. ambrosettii*, than species that construct nests (e.g., *P. ambrosettii* and *H. watwata*). Thus, it is probable that the ethological component exerts an influence on the different degrees of ontogenetic development presented by newly hatched larvae.

CONCLUSIONS

The present results show that *Pterygoplichthys ambrosettii* has indirect development with a distinct post-larval stage following the larval stage. Newly hatched larvae exhibit a well-developed yolk sac and the absence of pigmentation. Characters such as odontodes posteriorly to the preopercle, the number of plates on lateral line, lower lip with three series of papillae, spots on the upper caudal fin ray, caudal fin similar to that of the adult, body ventrally covered with dermal plates and

odontodes, small irregular spots on the head, and typical ventral color pattern of adults undergo less change during development and can therefore be useful in taxonomical analyses. The morphometric data revealed that a large part of the variation in body proportions occurs during less advanced developmental stages. Parental care influences the ontogenetic development of newly hatched larvae.

Acknowledgments: The authors thank Arif Cais, Gilson L. Volpato, Lilian Casatti, Valdener Garutti, Dorotéia R. S. Souza, and Fernando R. Carvalho for their helpful suggestions concerning the manuscript. They also thank Antonio J. Manzato for the statistical orientation, Carlos Daghlian (in memoriam) for suggestions to improve the wording, Edilson Nascimento for technical support regarding the image quality, Richard Boike for revision of the writing, and anonymous reviewers for their valuable comments. This study received funding from National Council of Scientific and Technological Development (CNPq process 100.957/93-5) in the form of a grant to RBA.

Authors' contributions: RBA collected and analyzed the data, prepared the manuscript, and revised the drafts. FL contributed to the study design and performed the sample collections. Both authors approved the final manuscript.

Competing interests: The authors declare that they have no conflicts of interest.

Availability of data and materials: The data generated and analyzed during the present study are available from the corresponding author.

Consent for publication: Not applicable.

Ethics approval and consent to participate: Not applicable.

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