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Gill morphology and morphometry of the facultative air-breathing armoured catfish, *Corydoras paleatus*, in relation on aquatic respiration

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Abstract

The Neotropical armoured catfish *Corydoras paleatus* is a facultative air-breathing teleost commonly exported as ornamental fish. In this species, air breathing enables it to survive and inhabit freshwater environments with low oxygen levels. Therefore, it is important to analyse the gills from a morphological aspect and its dimensions in relation to body mass with reference to aquatic respiration. For that, the gills were analysed using a stereoscopic microscope for morphometric studies, and structural and ultrastructural studies were carried out to compare the four branchial arches. Furthermore, two immunohistochemical techniques were used to locate and identify the presence of a Na^+/K^+ pump. The characterization of the potential for cell proliferation of this organ was assessed using an anti-PCNA antibody. The results show that gills of *C. paleatus* present some characteristics related to its diet and lifestyle, such as the limited development of gill rakers and the abundance of taste buds. In addition, other special features associated with the environment and bimodal breathing were observed: scarce and absent mucous cells (MCs) in the gill filaments and branchial lamellae, respectively, and the localization of mitochondria-rich cells (MRCs) covering the basal third of the branchial lamellae, which reduces the gill respiratory area. A peculiar finding in the gill epithelium of this armoured catfish was the presence of mononuclear cells with sarcomeres similar to myoid cells, whose functional importance should be determined in future studies. Finally, in *C. paleatus*, the interlamellar space of gill filaments is an important site for cell turnover and ionoregulation; the latter function is also performed by the branchial lamellae.

KEYWORDS
armoured catfish, bimodal respiration, morphometric analysis, PCNA, Na^+/K^+ ATPase

1 | INTRODUCTION

In fishes, the main mode of gas exchange is branchial. Nonetheless, the gills of teleost in addition to participating in respiration perform functions in transport and ion exchange, excretion of nitrogenous waste products and the maintenance of acid–base balance (Fernandes *et al*., 1998; Goss *et al*., 1998; Sturla *et al*., 2001; Evans *et al*., 2005). All these functions are performed by the epithelia of gill filaments and branchial lamellae. Among other cells, the gills contain mucous cells (MCs) and mitochondria-rich cells (MRCs), the latter having a high metabolic potential in the ion transport evidenced by ATPases (Díaz *et al*., 2001, 2005a; Olson, 2000; Vigliano *et al*., 2006). In addition, a great diversity of teleost has accessory adaptations for aerial respiration (Fernandes *et al*., 1994; Graham & Wegner, 2009; Hakim *et al*., 1978; Hughes *et al*., 1973; Hughes & Al-Kadhomiy, 1986; Perna & Fernandes, 1996; Santos *et al*., 1994). The Neotropical armoured catfish, *Corydoras paleatus* (Jenyns, 1842), presents double air-breathing (Ringuelet, 1975) by extracting oxygen from the water and the air, for which it uses,

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respectively, its gills and its intestine. The existence of adaptations in the last portion of the intestine that allow gas exchange from air ingestion has been described by Plaul *et al.* (2016a, 2016b).

C. paleatus (Siluriformes, Callichthyidae) is a benthic fish found in freshwater environments, which can contain very low oxygen concentrations (Kramer, 1987), and can be found in southern Brazil, Paraguay, Uruguay and northern and central Argentina. According to Panné Huidobro (2014), in Argentina, *Corydoras* sp. is one of the most commonly exported teleost as ornamental fish.

Thus, the goal of this study was to analyse the morphology of the gills of armoured catfish specimens and the cell types present in them through histology, electron microscopy and immunohistochemical techniques. Furthermore, the gill dimensions in relation to body mass were investigated, with special reference to aquatic respiration compared to other teleost species. Despite its importance as an aquarium species and the peculiarity of having double air-breathing, there are few studies on the respiratory system (Fanta *et al.*, 2003; Pesce *et al.*, 2008).

2 | MATERIALS AND METHODS

The specimens used in this study were collected according to the Ethics Committee for the Use of Animals (CICUAL) of FCV, UNLP, animal welfare laws, guidelines and policies as approved by the CD and FCV under the protocol number 129/09.

2.1 | Specimen sampling

A total of 25 healthy adult specimens of *C. paleatus* were collected from streams situated in the La Plata city (Buenos Aires, Argentina). Fish were transported alive to the authors' laboratory, kept in a tank at 22 ± 2°C with a pH of 7.0 for at least 3 weeks, and fed with commercial food for bottom feeders (TetraMin®Tropical Tablets, Melle, Germany). Fish were euthanized by anaesthetic overdose (30 mg l^{-1} Eugenol solution) following García-Gómez *et al.* (2002). Eugenol is a safe and effective anaesthetic that reduces stress level of fishes, which is widely used in aquaculture studies, but the FDA has not recommended it for animals of consumption because of the adverse effects on flavour (Purbosari *et al.*, 2019; Raissy & Ansari, 2011).

2.2 | Morphological and morphometric analysis

Immediately, the armoured catfish were weighed (4.7 ± 1.35 g, mean ± S.D.), measured (5.85 ± 1.08 cm, mean total length ± S.D.) and then each branchial arch (Ba) was isolated and termed, from lateral to medial, as first (BaI), second (BaII), third (BaIII) and fourth (BaIV) (Figure 1). Samples were fixed by immersion in 10% buffered formalin, and they were observed under a stereoscopic microscope (Kyowa, model SZM 800N, Nikon) and used for morphometric studies of Ba and gill filaments. The morphometric measurements of eight of the collected specimens were made following the techniques of Gray (1954) and Hughes (1966, 1984): Filaments on both sides (X4) = Total gill filaments; Average filament length (mm); Total length for all filaments (L); Branchial lamellae per mm (l/d′); Distance between branchial lamellae (d); Surface area of branchial lamellae (SLA); Bilateral area (bl): SLA * 2; Total surface area: (L) × l/d′ × bl; Total surface area per body mass: Total surface area/Average weight.

2.3 | Histological methods

For light microscopy, gill samples were prepared according to the standard protocol and then stained with routine techniques: haematoxylin–eosin and Masson's trichrome methods. To characterize the MCs, sections of tissues were subjected to diverse histochemistry techniques (Table 1). The results were evaluated according to the intensity of the reactions (0, negative; 1, light; 2, moderate; 3, strong). These scores were established according to previous histochemical studies (Plaul *et al.*, 2016b).

2.4 | Immunohistochemical techniques

Cell proliferation (PCNA) and Na^+/K^+ ATPase (NKP) expression were evaluated by immunohistochemistry. For this, histology slides (3 μm) were incubated with anti-PCNA antibody (mouse monoclonal clone PC 10, ascites fluid; Sigma Chemical, St. Louis, MO, USA; 1:3000) and with anti-NKP antibody (mouse monoclonal DSHB Developmental Studies Hybridoma Bank, clone SP2/0Ag8; 1:200) respectively. Liquid DAB (DakoVR Cytomation) was used as chromogen and haematoxylin

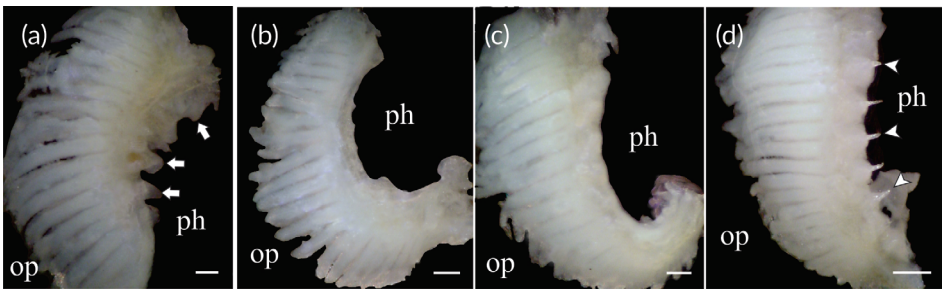

FIGURE 1 The four separate gills in catfish, *Corydoras paleatus*, arranged from left to right. This picture was taken post fixation. (a) The first branchial arch (BaI) showing a high development of conical epithelial protuberances (arrows). (b) and (c) The second (BaII) and third (BaIII) branchial arches. (d) The fourth branchial arch (BaIV) showing gill rakers (arrowheads). op: opercular side, ph: pharyngeal side. Scale bar: 1 mm

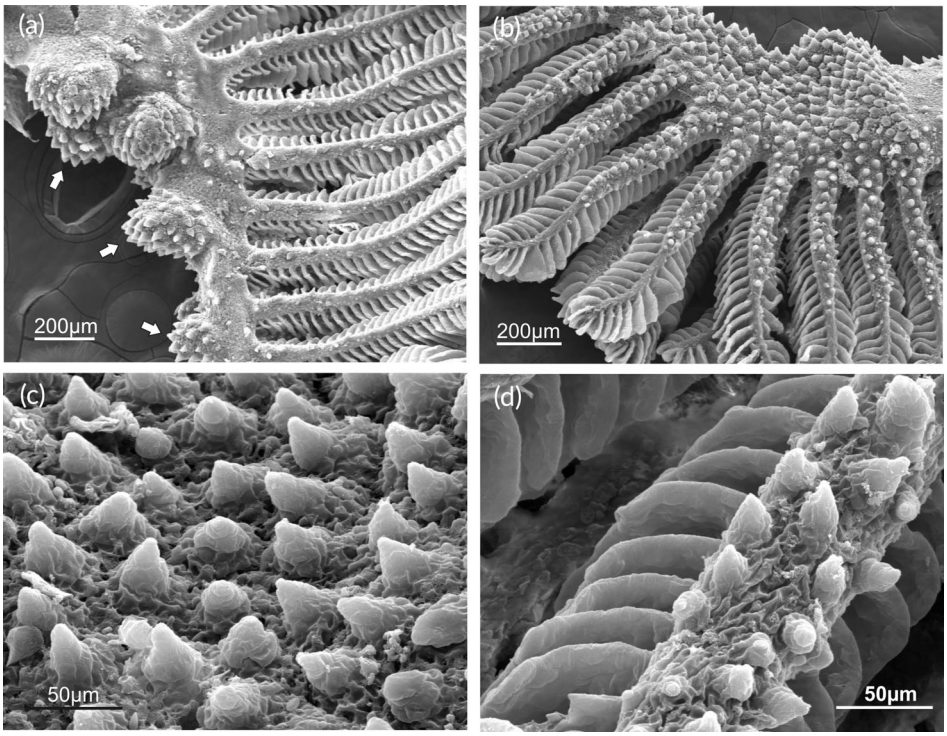

FIGURE 2 Scanning electron photomicrographs of the gills. (a) First branchial arch showing epithelial protuberances with taste buds (arrows). (b) Distribution of taste buds on the second branchial arch. (c) and (d) The epithelium of the branchial arch and gill filament, respectively, showing the epithelial cells with characteristic pattern on the surface and taste buds

TABLE 1 Histochemical procedures for visualizing and identifying GCs in the mucous cells of *Corydoras paleatus*

Procedures	Interpretation of staining reactions	References
PAS	Glycoconjugates with oxidizable vicinal diols and/or glycogen	Mc Manus (1948)
PAPS	Sialic acid residues	Reid *et al*. (1973)
AB pH 2.5	Glycoconjugates with carboxyl groups (sialic acid or uronic acid) and/or with *O*-sulphate esters	Lev and Spicer (1964)
AB pH 1.0	Glycoconjugates with *O*-sulphate esters	Lev and Spicer (1964)
AB pH 0.5	Very sulphated glycoconjugates	Lev and Spicer (1964)
TB pH 5.6	Glycoconjugates with *O*-sulphate esters and carboxyl groups	Lison (1953)
TB pH 4.2	Glycoconjugates with *O*-sulphate esters	Lison (1953)

for counterstaining. As negative control, samples were processed in a similar way but omitting the primary antibody. As a positive control, PCNA samples of mouse and rabbit intestine were used. For the positive control for NKP, a chicken kidney sample was used (Plaul *et al*., 2016a). Micrographs were taken with an Olympus microscope (model CX31) equipped with an Olympus camera (model U-CMAD3, Tokyo, Japan).

2.5 | Scanning electron microscopy (SEM) and transmission (TEM) electron microscopy

Samples of gills were fixed in cold 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.0) for 4 h at 4°C. For SEM analysis, a Philips SEM 505 microscope and Soft Imaging System ADDA II (SIS) software were used, which belongs to CINDECA, School of Exact Sciences, National University of La Plata (UNLP). For TEM, small pieces of gills were embedded in Epon 812. Semi-thin sections, obtained from the epoxy resin blocks and stained with toluidine blue, were used to select areas for thin sectioning. Thin sections (60 nm) were stained with uranile acetate and lead citrate. Studies were performed with a JEOL JEM 1200-EXII electron microscope belonging to the School of Veterinary Sciences, UNLP.

3 | RESULTS

3.1 | General structure

In the gills of *C. paleatus*, each holobranch consisted of an arch displaying caudally a curvature angle. This curvature was observed in the centre of BaI and BaII, whereas in the remaining arches, it was found in the upper third portion (Figure 1a–d). BaI was characterized by the presence of highly developed conical epithelial protuberances (Figure 1a), and in BaIV,

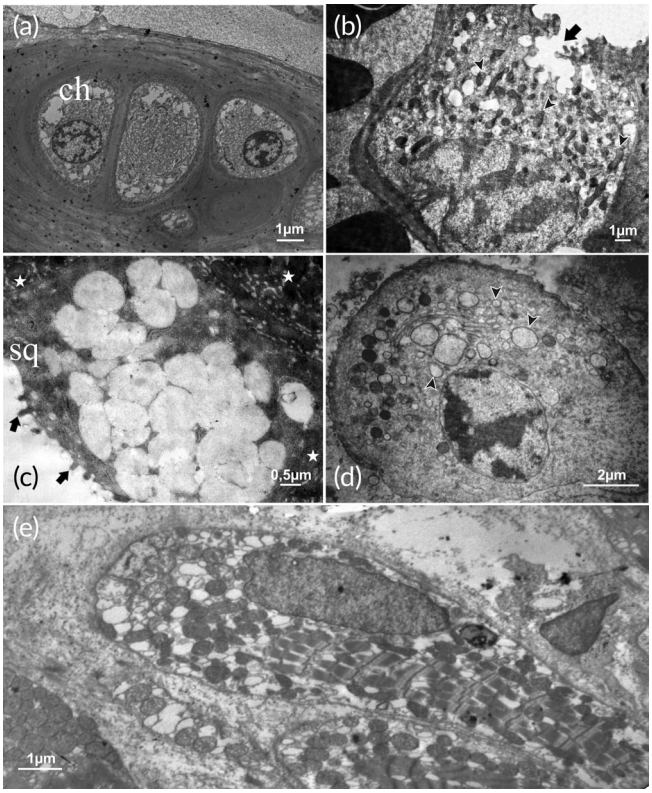

FIGURE 3 Transmission electron micrographs of a gill filament. (a) Photomicrograph to show the hyaline cartilage. Note the chondrocytes (ch) forming an isogenous group. (b) A mitochondria-rich cell (MRC) contacting the free surface with a concave apical crypt (arrow). The arrowheads point to mitochondria. (c) A mucous cell (MC) surrounded by MRC (stars) and a squamous cells (sq) located in the superficial layers of the epithelium. Note the apical projections of the plasma membrane (arrows). (d) Neuroepithelial cell with vesicles (arrowheads) with different diameters. (e) Myoid cell with a sarcomere-like structure in their cytoplasm

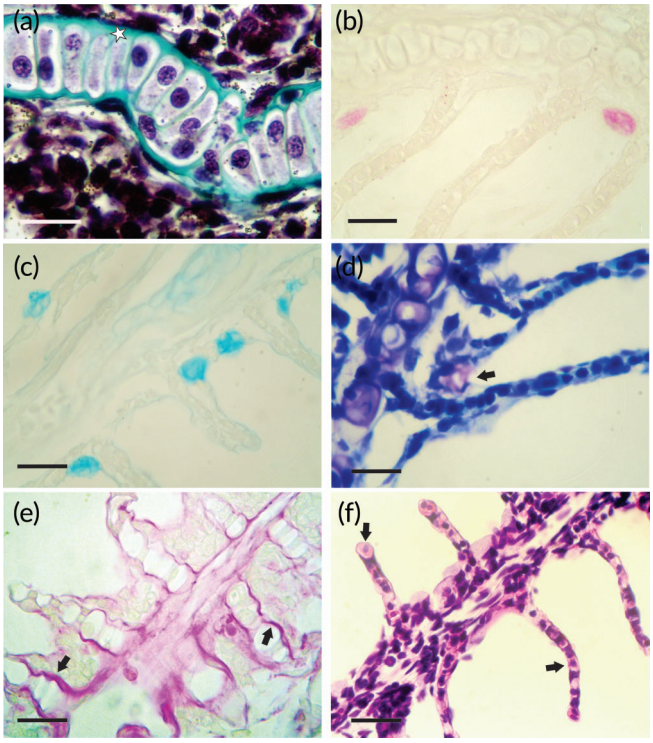

FIGURE 4 Histological aspect of gills with different staining techniques. (a) Hyaline cartilage with Masson's trichrome method; note the thick perichondrium (star). (b) Moderate reaction in the mucous cells (MCs), PAPS technique. (c) MCs positive with AB pH 2.5 method. (d) Metachromatic reaction of GCs is observed (arrow). TB pH 5.6 technique. (e) A thick basal membrane (arrows) surrounding the pillar cells, PAS method. (f) Lamellar capillaries (arrows), haematoxylin–eosin method. Scale bar: 20 μm

short and widely spaced gill rakers were observed (Figure 1d). In addition, in the epithelium of branchial arches, protuberances and gill filaments showed abundant taste buds (Figure 2a–d).

In the gills, a stratified epithelium can be identified covering the branchial arches and gill filaments. Each filament presented 29 branchial lamellae per millimetre and radiate out from the dorsal and ventral surfaces. Gill filament was composed an axis of hyaline cartilaginous tissue (Figure 3a) with scarce intercellular substance and a thick perichondrium (Figure 4a). In the epithelium of the gill filament, a variable number of cell types can be observed, such as MRCs (Figure 3b), MCs (Figure 3c), neuroepithelial cells (Figure 3d), squamous epithelial cells and stem cells, among others. The branchial lamellae were formed by two cellular layers. Internally, pillar cells were arranged forming the perpendicular axis surrounded by the lumen of the blood capillaries. The outer layer was a continuous simple squamous epithelium.

MCs were located mainly in the interlamellar space of gill filaments. Histochemical techniques showed the presence of abundant and diverse glycoconjugates (GCs) (Table 2; Figure 4b–d). MRCs were difficult to differentiate using routine techniques. The TEM micrographs showed an extensive system of intracellular canaliculi associated with a large number of mitochondria (Figure 3b). Neuroepithelial cells were scarce; occurring between the other epithelium cells, under TEM micrographs, these cells showed a pyriform shape with an electron-lucid cytoplasm, which contains a highly developed Golgi complex and vesicles arranged around it (Figure 3d). With TEM, another cell type has been detected in the epithelium characterized by the presence of a sarcomere-like structure in their cytoplasm (Figure 3e). They were found as isolated cells among the other epithelial cells, being elongated in shape, with an elongated and euchromatic peripheral nucleus, and containing a large amount of mitochondria in the end of the cell.

Pillar cells had a cuboidal shape with scarce cytoplasm and a central rounded euchromatic nucleus. A PAS-positive basal membrane surrounded these cells and their projections entirely (Figure 4e). Pillar cells were characterized by the presence of thin cytoplasmic projections on their ends that, together with the projections of adjacent cells, form the walls of the lamellar capillaries (Figures 4f and 5a). TEM micrographs showed that the cytoplasmic projections were joined by occlusive junctions and that at the end of the branchial lamellae, the cytoplasmic projections of the pillar cells were joined forming a

TABLE 2 Histochemical analysis of the mucous cells

	Histochemical techniques						
	PAS	PAPS	AB pH 2.5	AB pH 1.0	AB pH 0.5	TB pH 5.6	TB pH 4.2
MCs	3	1/2	3	3	2/3	3 m	3 m

Notes. PAS: periodic acid Schiff reagent, PAPS: sialic acid residues, AB pH 2.5: GCs with carboxyl groups (sialic acid or uronic acid) and/or with *O*-sulphate esters, AB pH 1.0: GCs with *O*-sulphate esters, AB pH 0.5: very sulphated GCs, TB pH 5.6: GCs with *O*-sulphate esters and carboxyl groups and TB pH 4.2: GCs with *O*-sulphate esters.
m: metachromasia; MCs: mucous cells.

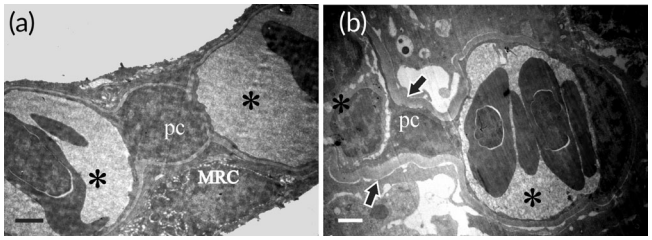

FIGURE 5 Transmission electron micrographs of branchial lamellae. (a) This photomicrograph shows lamellar capillaries (asterisks) formed by the cytoplasmic projections of two pillar cells (pc). Note the intercalated position of mitochondria-rich cell (MRC) between capillary vessels in the epithelium. (b) Tip of branchial lamellae; note the prominent basal lamina (arrows) contacting at both sides of the lamellar capillaries. Scale bar: 2 μm

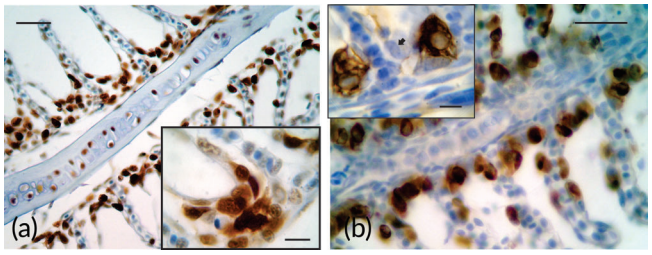

FIGURE 6 Immunohistochemical characterization of gills of *Corydoras paleatus*. (a) PCNA antibody shows a high positivity in the interlamellar space of gill filaments. Scale bar: 40 μm. Inset: Higher magnification of the interlamellar spaces showing an intense labelling in the majority of the nuclei. Scale bar: 10 μm. (b) Panoramic view of the gill filament showing intense immunostaining of mitochondria-rich cells (MRCs). Scale bar: 40 μm. Inset: Higher magnification of the interlamellar spaces showing an intense labelling in the entire MRCs; the arrow indicates the nucleus of outer epithelial cell. Scale bar: 10 μm

capillary of a larger diameter (Figure 5b). Outer epithelial cells externally formed a continuous epithelial layer and occurred in intimate contact with the pillar cells, although both separated by a basal lamina.

3.2 | Immunohistochemistry techniques

A great immunoreactivity for PCNA was found in the nuclei of chondrocytes in the hyaline cartilage, and a high positivity throughout the epithelium of the gill filament interlamellar space (Figure 6a). The response pattern for NKP-positivity was strong and homogeneous in the cells located in the gill filament's interlamellar space and in the outer epithelium of the basal third of the branchial lamellae (Figure 6b).

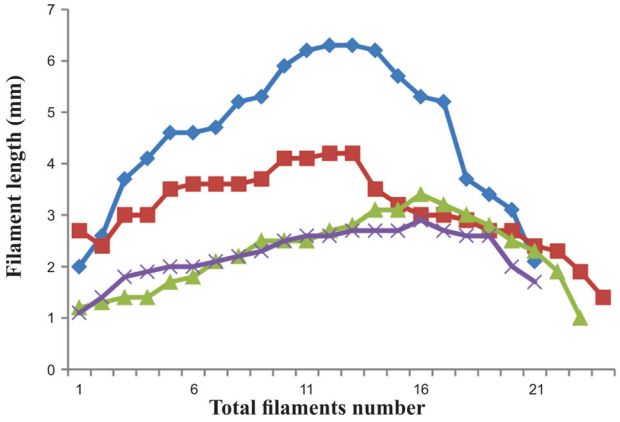

FIGURE 7 Graph showing variation in filament length when plotted for hemibranchs of different gill arch (BqI, BqII, BqIII, BqIV)

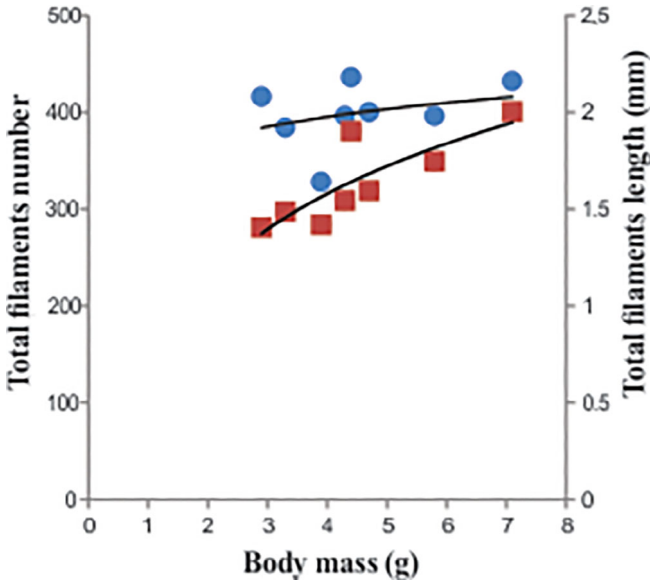

FIGURE 8 Relationships between total filament number/total filament length and body mass of *Corydoras paleatus* (●Body mass/Total filament number, ■ Body mass/Total filament length)

TABLE 3 Measurements of the gills of *Corydoras paleatus*

Gill measurements	
Total surface area	471.018 mm^2
Total surface area per body mass	100.22 $mm^2\ g^{-1}$
Gill filaments	
Total gill filaments	398.5
Average filament length	1.64 mm
Total length for all filaments	1082.8 mm
Branchial lamellae	
Branchial lamellae per mm	29
Distance between branchial lamellae	0.026 mm
Surface area of branchial lamellae	0.0075 mm^2

TABLE 4 Total respiratory surface area of the gills of several species of teleosts

Species	Total respiratory surface area ($mm^2\ g^{-1}$)	References
Bentonic species		
Pleuronectes platessa	433	Hughes, 1966
Trigla gurnadus	224	Hughes, 1966
Callionymus lyra	168	Hughes, 1966
Air-breathing species		
Anabas testudineus	556	Hughes *et al*., 1973
Channa punctata	470	Hakim *et al*., 1978
Boleophthalmus boddarti	93	Hughes & Al-Kadhomiy, 1986
Hoplerythrinus unitaeniatus	599	Fernandes *et al*., 1994
Rhinelepis strigosa	616	Santos *et al*., 1994
Hypostomus plecostomus	436	Perna & Fernandes, 1996
Corydoras paleatus	100	Present study

3.3 | Gill morphometry

The total number of filaments per hemibranch was in general constant. In the four gill arches, the shortest filaments were those on the ends. The longest filaments were found in BaI and the shortest ones in BaIII and BaIV (Figure 7). The relationship between the total number and length of filaments was directly proportional to the body mass (Figure 8). The results of the morphometric analysis of the gills are presented in Table 3.

4 | DISCUSSION

4.1 | Gill structure

The genus *Corydoras* (Lacépède) has a well-developed respiratory capacity (Kramer & McClure, 1980) that enables it to survive in and inhabit freshwater environments with low oxygen levels. The development of a mechanism to perform gas exchange with air is an important adaptive mechanism for life in a hypoxia-prone habitat (Plaul *et al*., 2016a, 2016b). *C. paleatus* is a bimodal breather species and has been considered a facultative air-breathing teleost. Gómez (1993) has shown its ability to survive for at least 14 days (under experimental conditions) when it is prevented from ascending to the surface. Although the gill arch's general organization in *C. paleatus* was similar to that previously described for other species of teleost (Díaz *et al*., 2009; Elsheikh, 2013; Grizzle & Rogers, 1976; Hibiya, 1982; Hughes, 1984; Srivastava *et al*., 2012; Vigliano *et al*., 2006; Wilson & Laurent, 2002), it presents some variations possibly because of its habitat and bimodal mode of respiration.

4.2 | Habitat and feeding style

The number and shape of gill rakers in teleosts are related to the diet. In benthic feeder fishes, they are generally short, whereas in zooplanktivorous fishes they are long (Bertin, 1958; Hyatt, 1979; Matthes, 1963; Vandewalle *et al*., 2000). The scarce development and widely spaced gill rakers in only one branchial arch indicate that *C. paleatus* is exclusively a benthic feeder. Besides, the number and distribution of taste buds vary greatly according to the species. In general, benthic and nocturnal fishes present a great density of taste buds in all body surfaces. Instead, open water species or surface feeders present them only in some areas of the palate (Hara *et al*., 1994; Marui *et al*., 1983; Morais, 2017). *C. paleatus* have abundant taste buds not only on both sides of gills arches but also in its head and body's ventral surface (data not shown). This pattern of distribution indicates that the food selection in this species is done through chemical receptors.

4.3 | Gill epithelium

The presence of MCs in the gill filaments is a common feature in teleosts, but their distribution and abundance vary among species (Díaz *et al*., 2001, 2005a, 2005b, 2010; Tano de la Hoz *et al*., 2014). In accordance with previous observations by Wilson and Laurent (2002) for other teleosts, *C. paleatus* presents scarce MCs in the gill filaments, and this cell type is not found in the branchial lamellae, a feature that could be associated with their benthic habitat. Various functions have been postulated for mucus: if it is rich in sulphates, as was shown in *C. paleatus* by the high intensity of AB pH 1 staining, it can form a barrier on the epithelial tissue of the gill that prevents the loss of ions and reduces the environmental osmolality (Handy, 1989; Powell *et al*., 1994). It has lubricating properties (Yashpal *et al*., 2007) and may prevent the increase of pathogenic microorganisms in the epithelial surfaces. Residues of sialic acids could be receptors that bind

ligands of microorganisms and, consequently, participate in immune regulation mechanisms (Schulte & Spicer, 1985).

Many studies have described MRCs in different teleosts with interspecific differential characteristics in their distribution, existence of subtypes, morphology and quantity (Monteiro *et al*., 2010; Pisam *et al*., 1995; Wilson & Laurent, 2002). TEM observations of these cells show the existence of numerous mitochondria and a complex system of tubules. These ultrastructural characteristics could be associated with an osmoregulatory function, considering high levels of energy necessary for ion transport. Observations using the anti-Na^+/K^+-ATPase antibody in these cells showed their localization. In *C. paleatus* MRCs are situated in the interlamellar space of gill filaments and in the branchial lamellae.

In the gill filaments of *C. paleatus*, neuroepithelial cells were found. These cells were identified because their morphology was very similar to those found in other teleosts, such as *Oncorhynchus mykiss* (Walbaum, 1792), *Stizoztedion lucioperca* (Linnaeus, 1758), *Ameiurus melas* (Rafinesque, 1820) (=*Ictalurus melas*), *Anguilla anguilla* (Linnaeus, 1758) (Dunel-Erb *et al*., 1982), *Hypostomus plecostomus* (Linnaeus, 1758) (Fernandes & Perna-Martins, 2001), *Coelorhinchus caelorhinchus* (Risso, 1810) (=*Coelorhynchus coelorhynchus*) (Calabró *et al*., 2005) and *Poecilia vivipara* Bloch & Schneider, 1801 (Borges de Oliveira *et al*., 2006). These cells probably fulfil the role of oxygen sensors and contribute to regulate blood flow (Sudin & Nilsson, 2002).

A very peculiar cell population found in the gill epithelium is constituted by cells that present the striation characteristic of skeletal and cardiac muscular tissue. The authors did not find references to mononuclear cells with well-defined sarcomeres in the gills of any species of teleost. Nonetheless, several researchers (Chan, 1992; Curtis *et al*., 1979; Jablonska-Mestanova *et al*., 2013; Raviola & Raviola, 1967) have observed and described cells with similar characteristics, called myoid cells, in the thymic medulla of mammals, birds, reptiles and amphibians. In the studies carried out on the thymus of *Neoceratodus forsteri* (Krefft, 1870) (Dipnoi, Ceratodontiformes) and *Oreochromis niloticus* (Linneo, 1758) (Perciformes, Cichlidae), Mohammad *et al*. (2007) and Cao *et al*. (2017) respectively, cells with similar characteristics to those found in the gill epithelium of *C. paleatus* were observed. The embryological origin of these thymic cells is controversial; some studies propose that they derive from the neural crest (Bódi *et al*., 2015). Its origin from the prechordal mesoderm was also considered (Seifert & Christ, 1990). Nonetheless, the existence of tumours of the thymic epithelial cells, in which differentiation patterns towards striated muscle are found, raises the possibility of a common origin between the epithelial reticular cells and the myoid cells of the thymus (Kalhor & Moran, 2019; Murakami *et al*., 1984). Considering that the gill and thymic epithelia derive from the pharyngeal pouches, it could be possible that a similar differentiation towards a myoid pattern occurs by the stem cells in the gill epithelium. The biological roles of these myoid cells in the thymus are not yet clear (Varga *et al*., 2019). Although several hypotheses have been made for these cells, the authors will highlight two of them: (a) the release of several biologically active substances (probably cytokines) in their environment that stimulate the growth and proliferation of macrophages and lymphocytes (Kamo *et al*., 1985), and (b) the function as myoblasts and the ability to regenerate postnatal skeletal muscle when thymic myoid cells are found *in vitro* (Pagel *et al*., 2000).

In the gills, stem cells are found in the basal and intermediate layers of the gill epithelium (Wilson & Laurent, 2002). The increase in the cellular proliferation and the migration of cells towards the branchial lamella are important gill adaptation mechanisms to changes in the environment (Dang *et al*., 2000; Handy, 2003; Velasco Santamaría *et al*., 2006). In numerous freshwater species, the expression of PCNA in gill epithelium has been shown. Chrétien and Pisam (1986), Laurent *et al*. (1994) and Monteiro *et al*. (2009) observed proliferative activity in both the gill filaments as in the branchial lamellae. In *C. paleatus*, immunoreactivity of PCNA was observed especially in interlamellar spaces of gill filaments, coinciding with the observations in *Poecilia reticulata* Peters 1859 (Chrétien & Pisam, 1986), *O. mykiss* (Laurent *et al*., 1994), *Oncorhynchus keta* (Walbaum, 1792) (Uchida *et al*., 1996), *Oreochromis mossambicus* (Peters 1852) (Dang *et al*., 2000) and *Pymelodus albicans* (Valenciennes 1840) (Pastor *et al*., 2008).

The structure of the branchial lamellae of *C. paleatus* specimens was similar to that previously described in different species of teleost (Hughes, 1984; Wilson & Laurent, 2002). Pillar cells are type of endothelial cells that form the walls of the lamellar capillaries (Díaz *et al*., 2009; Hughes & Grimstone, 1965; Vigliano *et al*., 2006; Wilson & Laurent, 2002). Nonetheless, a histological peculiarity, related to cell type distribution, was also found. As mentioned, MRCs are situated between the pillar cells and outer epithelial layer of the branchial lamellae. According to Hirai *et al*. (1999), the occurrence of MRCs in this last localization would be a physiological adaptation to increase ion absorption in some teleosts.

4.4 | Gill morphometry

According to Hughes (1980), fishes with bimodal respiration present a reduced respiratory gill area, and it is correlated with potential oxygen loss or carbon dioxide uptake in hypoxia prone habitats. If we compare the total gill respiratory surface area of *C. paleatus* with other benthic fish with and without bimodal respiration (Table 4), we observe that only *Boleophthalmus boddarti* (Pallas, 1770) and *C. paleatus* have a smaller respiratory surface area. It seems obvious that the respiratory surface area increases with body mass, but the measurements of gill filaments and the branchial lamellae can vary quite among species, and this variability is closely related to the habitat and the mode of life (Fernandes *et al*., 1994). According to Brauner and Rombough (2012), air-breathing fishes have a reduced mass-specific total gill surface area relative to non-air-breathers, which is a result of having both fewer and smaller gill filaments and branchial lamellae. Comparing *C. paleatus* and the air-breathing teleosts studied by Hughes *et al*. (1973), Hakim *et al*. (1978) and Hughes and Al-Kadhomiy (1986), *C. paleatus* has a higher number of branchial

lamellae per millimetre of gill filament. Perna and Fernandes (1996) observed the same in *H. plecostomus*. According to these researchers, this characteristic would imply a reduced dead space, which would favour the diffusion of oxygen from water to blood. Hughes and Al-Kadhomiy (1986) indicated the importance of considering the thickness of the tissue found between water and blood and the interchange of oxygen and other gases. If we consider that in both *B. boddarti* and *C. paleatus* the MRCs are found covering the basal third of the branchial lamellae, the total gill respiratory surface area is even slightly smaller than that calculated. Plaul *et al*. (2016a, 2016b) found distinctive features of the intestinal mucosa of *C. paleatus* in its caudal sector in relation to gas exchange such as absence of villi, presence of air bubbles and a very thin wall formed by squamous enterocytes in close contact with the capillary network. The blood capillaries were separated by a basal lamina of enterocytes. For these reasons, the authors believe that complementation with air-breathing is very important, and that gills have an intense osmoregulatory activity.

At present, all the monitoring plans for water bodies include fish as indicators of environmental pollution. The gills are the site of contact with environmental contaminants. Nonetheless, there is a scarcity of works which analysed the gill in relation to cell renovation. The anti-PCNA antibody recognized in *C. paleatus* for different cell populations showed great proliferative activity in the gills. The morphometric study performed in this work included only adult individuals, and it was observed that the total gill respiratory surface has a smaller area compared with other air-breathing fishes.

In conclusion, these results show that *C. paleatus* gills are characterized by some peculiarities related to the diet, such as the limited development of gill rakers and the abundance of taste buds. In addition, other special characteristics associated with the environment and bimodal breather were observed, such as scarce and absent MCs in the gill filaments and branchial lamellae, respectively, and the localization of MRCs covering the basal third of the branchial lamellae, further reducing the gill respiratory area. Despite the fact that *C. paleatus* is considered a facultative air-breathing teleost (as species listed in Table 4), the lack of long-term aerial respiration causes the death of the specimen. The presence of myoid cells with sarcomeres similar to myoblasts in the gill epithelium is a unique feature of this species. The functional importance and origin of these cells should be determined in future studies. Finally, in *C. paleatus*, the interlamellar spaces of gill filaments are important sites for cell turnover and ionoregulation, being that the latter function is also performed by the branchial lamellae.

AUTHOR CONTRIBUTIONS

All authors contributed to manuscript preparation. S.E.P.: fish collection, project conception and design, and data analysis; A.O.D.: data collection, data analysis and interpretation of data; C.G.B.: interpretation of data and funding.

DATA AVAILABILITY STATEMENT

None.

REFERENCES

Bertin, L. (1958). Appareil digestif. In P. P. Grassé (Ed.), *Traité de Zoologie* (Vol. 13 (fasc. 2), pp. 1249–1302). Paris, France: Masson.

Bódi, I., Minkó, K., Molnár, D., Nagy, N., & Oláh, I. (2015). A novel aspect of the structure of the avian thymic medulla. *Cell and Tissue Research*, *359*, 489–501. https://doi.org/10.1007/s00441-014-2027-1.

Borges de Oliveira, R., Vieira Rosa, E., do Nascimento, V., Neves Menezes-Faria, J. C., Vigário, A. F., Marinho Vieira, P., … de Sousa Menezes, J. (2006). Detection of paraneuronal cells in guppy (*Poecilia vivipara*) gill filament epithelium determined by histochemistry and transmission electron microscopy. *Revista de Biologia Neotropical*, *3*, 169–176.

Brauner, C. J., & Rombough, P. J. (2012). Ontogeny and paleophysiology of the gill: New insights from larval and air-breathing fish. *Respiratory Physiology & Neurobiology*, *184*, 293–300.

Calabró, C., Albanese, M. P., Lauriano, E. R., Martella, S., & Licata, A. (2005). Morphological, histochemical and immunohistochemical study of the gill epithelium in the abyssal teleost fish *Coelorhynchus coelorhynchus*. *Folia Histochemica et Cytobiologica*, *43*, 51–56.

Cao, J., Chen, Q., Lu, M., Hu, X., & Wang, M. (2017). Histology and ultrastructure of the thymus during development in tilapia, *Oreochromis niloticus*. *Journal of Anatomy*, *230*, 720–733. https://doi.org/10.1111/joa.12597.

Chan, A. S. (1992). Association of nerve fibres with myoid cells in the chick thymus. *Journal of Anatomy*, *181*, 509–512.

Chrétien, M., & Pisam, M. (1986). Cell renewal and differentiation in the gill epithelium of fresh or saltwater adapted euryhaline fish as revealed by [^{3}H] thymidine radioautography. *Biology of the Cell*, *56*, 137–150.

Curtis, S. K., Cowden, R. R., & Nagel, J. W. (1979). Ultrastructural and histochemical features of the thymus glands of the adult lungless salamander, *Plethodon glutinosus* (Caudata: Plethodontidae). *Journal of Morphology*, *160*, 241–274. https://doi.org/10.1002/jmor.1051600302.

Dang, Z., Lock, R. A. C., Flik, G., & Wendelaar-Bonga, S. E. (2000). Na^+/K^+-ATPase immunoreactivity in branchial chloride cells of *Oreochromis mossambicus* exposed to copper. *Journal of Experimental Biology*, *203*, 379–387.

Díaz, A. O., García, A. M., Devincenti, C. V., & Goldemberg, A. L. (2001). Mucous cells in *Micropogonias furnieri* gills: Histochemistry and ultrastructure. *Anatomia, Histologia, Embryologia*, *30*, 135–139.

Díaz, A. O., García, A. M., Devincenti, C. V., & Goldemberg, A. L. (2005b). Ultrastructure and histochemical study of glycoconjugates in the gills of the white croaker (*Micropogonias furnieri*). *Anatomia, Histologia, Embryologia*, *34*, 117–122.

Díaz, A. O., García, A. M., Escalante, A. H., & Goldemberg, A. L. (2010). Glycoproteins histochemistry of the gills of *Odontesthes bonariensis* (Teleostei, Atherinopsidae). *Journal of Fish Biology*, *77*, 1665–1673.

Díaz, A. O., García, A. M., & Goldemberg, A. L. (2005a). Glycoconjugates in the branchial mucous cells of *Cynoscion guatucupa* (Cuvier, 1830) (Pisces: Sciaenidae). *Scientia Marina*, *69*, 545–553.

Díaz, A. O., González Castro, M., García, A. M., Díaz de Astarloa, J. M., & Figueroa, D. E. (2009). Gross morphology and surface ultrastructure of the gills of *Odontesthes argentinensis* (Actinopterygii, Atherinopsidae) from a Southwestern Atlantic coastal lagoon. *Tissue and Cell*, *41*, 193–198.

Dunel-Erb, S., Bailly, Y., & Laurent, P. (1982). Neuroepithelial cells in fish gill primary lamellae. *Journal of Applied Physiology*, *53*, 1342–1353.

Elsheikh, E. H. (2013). Scanning electron microscopic studies of gill arches and rakers in relation to feeding habits of some freshwater fishes. *The Journal of Basic and Applied Zoology*, *66*, 121–130.

Evans, D. H., Piermarini, P. M., & Choe, K. P. (2005). The multifunctional fish gill: Dominant site of gas exchange, osmoregulation, acid-base regulation, and excretion of nitrogenous waste. *Physiological Reviews*, *85*, 97–177.

Fanta, E., Ríos, F. S. A., Romão, S., Casagrande Vianna, A. C., & Freiberger, S. (2003). Histopathology of the fish *Corydoras paleatus*

contaminated with sublethal levels of organophosphorus in water and food. *Ecotoxicology and Environmental Safety*, *54*, 119–130.

Fernandes, M. N., & Perna-Martins, S. A. (2001). Epithelial gill cells in the armored catfish, *Hypostomus cf. plecostomus* (Loricariidae). *Revista Brasileira de Biologia*, *61*, 69–78.

Fernandes, M. N., Perna-Martins, S. A., & Moron, S. E. (1998). Chloride cell apical surface changes in gill epithelia of the armoured catfish *Hypostomus plecostomus* during exposure to distilled water. *Journal of Fish Biology*, *52*, 844–849.

Fernandes, M. N., Rantin, F. T., Kalinin, A. L., & Moron, S. E. (1994). Comparative study of gill dimensions of three erythrinid species in relation to their respiratory function. *Canadian Journal of Zoology*, *72*, 160–165.

García-Gómez, A., de la Gándara, F., & Raja, T. (2002). Utilización del aceite de clavo, *Syzygiu aromaticum* L. (Merr. & Perry), como anestésico eficaz y económico para labores rutinarias de manipulación de peces marinos cultivados. *Boletín del Instituto Español de Oceanografía*, *18*, 21–23.

Gómez, S. E. (1993). Concentración letal de oxígeno disuelto para *Corydoras paleatus* y *Pimelodella laticeps* (Pisces, Siluriformes). *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Tomo VII*, *2*, 31–45.

Goss, G. G., Perry, S. F., Fryer, J. N., & Laurent, P. (1998). Gill morphology and acid-base regulation in freshwater fishes. *Comparative Biochemistry and Physiology*, *119A*, 107–115.

Graham, J. B., & Wegner, N. C. (2009). Breathing air in water and in air: The air-breathing fishes. In G. E. Nilsson (Ed.), *Respiratory physiology of vertebrates: Life with and without oxygen* (pp. 174–221). Oslo: Cambridge University Press.

Gray, I. E. (1954). Comparative study of the gill area of marine fishes. *Biology Bulletin*, *107*, 219–225.

Grizzle, J. M., & Rogers, W. A. (1976). *Anatomy and histology of the channel catfish* (p. 94). Alabama: Auburn Pinting Inc., Auburn University, Agricultural Experiment Station.

Hakim, A., Munshi, J. S. T., & Hughes, G. M. (1978). Morphometrics of the respiratory organs of the Indian green snakeheaded fish, *Channa punctata*. *Journal of Zoology*, *184*, 519–543.

Handy, R. D. (1989). The ionic composition of rainbow trout body mucus. *Comparative Biochemistry and Physiology*, *93A*, 571–575.

Handy, R. D. (2003). Chronic effects of copper exposure versus endocrine toxicity: Two sides of the same toxicological process? *Comparative Biochemistry and Physiology*, *135A*, 25–38.

Hara, T. J., Kitada, Y., & Evans, R. E. (1994). Distribution patterns of palatal taste buds and their responses to amino acids in salmonids. *Journal of Fish Biology*, *45*, 453–465.

Hibiya, H. (1982). *An atlas of fish histology. Normal and pathological features* (p. 147). Tokyo, Japan: Kodansha Ltd.

Hirai, N., Tagawa, M., Kaneko, T., Seika, T., & Tanaka, M. (1999). Distribution changes in branchial chloride cells during freshwater adaptation in Japanese sea bass *Iteolabrax japonicus*. *Zoological Science*, *16*, 43–49.

Hughes, G. M. (1966). The dimensions of fish gills in relation to their function. *Journal of Experimental Biology*, *45*, 177–195.

Hughes, G. M. (1980). Morphometry of fish gas exchange organs in relation to their respiratory function. In M. A. Ali (Ed.), *Environmental physiology of fishes* (pp. 33–56). New York, NY: Plenum Press.

Hughes, G. M. (1984). Measurement of gill area in fishes: Practices and problems. *Journal of the Marine Biological Association of the United Kingdom*, *64*, 637–655.

Hughes, G. M., & Al-Kadhomiy, N. K. (1986). Gill morphometry of the mudskipper, *Boleophthalmus boddarti*. *Journal of the Marine Biological Association of the United Kingdom*, *66*, 671–682.

Hughes, G. M., Dube, S. C., & Munshi, J. S. D. (1973). Surface area of the respiratory organs of the climbing perch, *Anabas testudineus* (Pisces: Anabantidae). *Journal of Zoology*, *170*, 227–243.

Hughes, G. M., & Grimstone, A. V. (1965). The fine structure of the secondary lamellae of the gills of *Gadus pollachius*. *Quarterly Journal of Microscopical Science*, *106*, 343–353.

Hyatt, K. D. (1979). Feeding strategy. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish physiology* (Vol. VIII, pp. 71–119). New York, NY: Academic Press.

Jablonska-Mestanova, V., Sisovsky, V., Danisovic, L., Polak, S., & Varga, I. (2013). The normal human newborns thymus. *Bratislavské Lekárske Listy*, *114*, 402–408.

Kalhor, N., & Moran, C. A. (2019). Thymic epithelial neoplasms with rhabdomyomatous component: A clinicopathological and immunohistochemical study of 7 cases. *Human Pathology*, *83*, 100–105. https://doi.org/10.1016/j.humpath.2018.08.027.

Kamo, I., Tada-Kikuchi, A., Furukawa, S., Iwasaki, Y., Nonaka, I., Satoyoshi, E., & Itoh, T. (1985). Effects of thymic myoid cell culture supernatant on cells from lymphatic tissues. *Cell Immunology*, *94*, 587–597.

Kramer, D. L. (1987). Dissolved oxygen and fish behavior. *Environmental Biology of Fishes*, *18*, 81–92.

Kramer, D. L., & McClure, M. (1980). Aerial respiration in the catfish, *Corydoras aeneus* (Callichthyidae). *Canadian Journal of Zoology*, *58*, 1984–1991.

Laurent, P., Dunel-Erb, S., Chevalier, C., & Lignon, J. (1994). Gill epithelial cells kinetics in a freshwater teleost, *Oncorhynchus mykiss* during adaptation to ion-poor water and hormonal treatments. *Fish Physiology and Biochemistry*, *13*, 353–370.

Lev, R., & Spicer, S. S. (1964). Specific staining of sulphate groups with alcian blue at low pH. *Journal of Histochemistry and Cytochemistry*, *12*, 309.

Lison, L. (1953). Histochimie et cytochimie animales. Principes et methods. In *Deuxième* (pp. 1–607). Paris, France: Gauthier-Villars.

Marui, T., Evans, R. E., Zielinski, B., & Hara, T. J. (1983). Gustatory responses of the rainbow trout (*Salmo gairdneri*) palate to amino acids and derivatives. *Journal of Comparative Physiology*, *153*, 423–433.

Matthes, H. M. (1963). A comparative study of the feeding mechanisms of some African Cyprinidae (Pisces, Cypriniformes). *Bijdragen tot de Dierkunde*, *33*, 3–35.

Mc Manus, J. F. A. (1948). Histological and histochemical uses of periodic acid. *Stain Technology*, *23*, 99–108.

Mohammad, M. G., Chilmonczyk, S., Birch, D., Aladaileh, S., Raftos, D., & Joss, J. (2007). Anatomy and cytology of the thymus in juvenile Australian lungfish, *Neoceratodus forsteri*. *Journal of Anatomy*, *211*, 784–797. https://doi.org/10.1111/j.1469-7580.2007.00814.x.

Monteiro, S. M., dos Santos, N. M. S., Calejo, M., Fontainhas-Fernandes, A., & Sousa, M. (2009). Copper toxicity in gills of the teleost fish *Oreochromis niloticus*: Effects in apoptosis induction and cell proliferation. *Aquatic Toxicology*, *94*, 219–228.

Monteiro, S. M., Oliveira, E., Fontaínhas-Fernandes, A., & Sousa, M. (2010). Fine structure of the branchial epithelium in the teleost *Oreochromis niloticus*. *Journal of Morphology*, *271*, 621–633.

Morais, S. (2017). The physiology of taste in fish: Potential implications for feeding stimulation and gut chemical sensing. *Reviews in Fisheries Science & Aquaculture*, *25*, 133–149. https://doi.org/10.1080/23308249.2016.1249279.

Murakami, S., Shamoto, M., Miura, K., & Takeuchi, J. (1984). A thymic tumor with massive proliferation of myoid cells. *Acta Pathologica Japonica*, *34*, 1375–1383. http://doi.org/10.1111/j.1440-1827.1984.tb00562.x.

Olson, K. R. (2000). Respiratory system. Microscopic functional anatomy. In G. K. Ostrander (Ed.), *The laboratory fish* (pp. 357–367). London, UK: Academic Press.

Pagel, C. N., Morgan, J. E., Gross, J. G., & Partridge, T. A. (2000). Thymic myoid cells as a source of cells for myoblast transfer. *Cell Transplantation*, *9*, 531–538.

Panné Huidobro, S. (2014). Comercio internacional de organismos acuáticos ornamentales: Participación Argentina en la importación y exportación 2012–2013. *Technical Report*. https://doi.org/10.13140/RG.2.1.1205.1369

Pastor, R., Sbodio, O., Galván, S. M., & Rossini, M. (2008). Correlación entre la expresión de dos biomarcadores (PCNA y Na^+/K^+ATPasa) en branquias del *Pymelodus albicans* de las cuencas del río Salado y Paraná. REDVET, IX, 1695–7504.

Perna, S. A., & Fernandes, M. N. (1996). Gill morphometry of the facultative air-breathing loricariid fish, *Hypostomus plecostomus* (Walbaum) with special emphasis on aquatic respiration. *Fish Physiology and Biochemistry*, *15*, 213–220.

Pesce, S. F., Cazenave, J., Monferrán, M. V., Frede, S., & Wunderlin, D. A. (2008). Integrated survey on toxic effects of lindane on neotropical fish: *Corydoras paleatus* and *Jenynsia multidentata*. *Environmental Pollution*, *156*, 775–783.

Pisam, M., Le Moal, C., Auperin, B., Prunet, P., & Rambourg, A. (1995). Apical structures of mitochondria-rich α and β cells in euryhaline fish gill: Their behaviour in various living conditions. *The Anatomical Record*, *241*, 13–24.

Plaul, S. E., Barbeito, C. G., & Díaz, A. O. (2016b). Histochemical differences along the intestine of *Corydoras paleatus* (Siluriformes, Callichthyidae). *Revista de Biología Tropical*, *64*, 343–356.

Plaul, S. E., Pastor, R., Díaz, A. O., & Barbeito, C. G. (2016a). Immunohistochemical and ultrastructure evidences for functional organization through the *Corydoras paleatus* intestine. *Microscopy Research and Technique*, *79*, 140–148.

Powell, M. D., Speare, D. J., & Wright, G. M. (1994). Comparative ultrastructural morphology of lamellar epithelial, chloride and mucous cell glycocalyx of the rainbow trout (*Oncorhynchus mykiss*) gill. *Journal of Fish Biology*, *44*, 725–730.

Purbosari, N., Warsiki, E., Syamsu, K., & Santoso, J. (2019). Natural versus synthetic anesthetic for transport of live fish: A review. *Aquaculture and Fisheries*, *4*, 129–133.

Raissy, M., & Ansari, M. (2011). Histopathological changes in the gills of naturally-infected *Capoeta aculeata* (Cuvier and Valenciennes, 1844) with parasites. *African Journal of Biotechnology*, *10*, 15422–15425.

Raviola, E., & Raviola, G. (1967). Striated muscle cells in the thymus of reptiles and birds: An electron microscopic study. *American Journal of Anatomy*, *121*, 623–645.

Reid, P. E., Culling, C. F. A., & Dunn, W. L. (1973). Saponification induced increase in the periodic acid Schiff reaction in the gastrointestinal tract. Mechanism and distribution of the reactive substance. *Journal of Histochemistry & Cytochemistry*, *21*, 473–483.

Ringuelet, R. A. (1975). Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. *Ecosur*, *2*, 1–122.

Santos, C. T. C., Fernandes, M. N., & Severi, W. (1994). Respiratory gill surface area of a facultative air-breathing loricariid fish, *Rhinelepis strigosa*. *Canadian Journal of Zoology*, *72*(2009), 2013.

Schulte, B. A., & Spicer, S. S. (1985). Histochemical methods for characterising secretory and cell surface sialo glycoconjugates. *Journal of Histochemistry and Cytochemistry*, *33*, 427–438.

Seifert, R., & Christ, B. (1990). On the differentiation and origin of myoid cells in the avian thymus. *Anatomy and Embryology (Berl)*, *181*, 287–298. https://doi.org/10.1007/BF00174622.

Srivastava, N., Kumari, U., KumariRai, A., Mittal, S., & Mittal, A. K. (2012). Histochemical analysis of glycoproteins in the gill epithelium of an Indian major carp, *Cirrhinus mrigala*. *Acta Histochemica*, *114*, 626–635.

Sturla, M., Masini, M. A., Prato, P., & Grattarola, C. (2001). Mitochondria-rich cells in gills and skin of an African lungfish, *Protopterus annectens*. *Cell and Tissue Research*, *303*, 351–358.

Sudin, L., & Nilsson, S. (2002). Branchial innervation. *Journal of Experimental Zoology*, *293*, 232–248.

Tano de la Hoz, M. F., García, A. M., González Castro, M., & Díaz, A. O. (2014). Histochemical and scanning electron microscopic approaches to gills in juveniles of *Odontesthes argentinensis* (Actinopterygii, Atherinopsidae). *International Journal of Aquatic Science*, *5*, 154–166.

Uchida, K., Kaneko, T., Yamauchi, K., & Hirano, T. (1996). Morphometrical analysis of chloride cell activity in the gill filaments and lamellae and changes in Na^+, K^+-ATPase activity during seawater adaptation in chum salmon fry. *Journal of Experimental Zoology*, *276*, 193–200.

Vandewalle, P., Parmentier, É., & Chardon, M. (2000). The branchial basket in teleost feeding. *Cybium*, *24*, 319–342.

Varga, I., Bódi, I., Kachlik, D., Mešťanová, V., & Klein, M. (2019). The enigmatic thymic myoid cells - their 130 years of history, embryonic origin, function and clinical significance. *Biologia*, *74*, 521–531.

Velasco Santamaría, Y. M., Gómez Manrique, W., & Calderón Bernal, J. M. (2006). Toxicidad aguda del sulfato de cobre ($CuSO_4$) en alevinos de Cachama Blanca (*Piaractus brachypomus*) bajo condiciones de aguas blandas. *Orinoquia*, *10*, 64–70.

Vigliano, F., Alemañ, N., Quiroga, M. I., & Nieto, J. M. (2006). Ultrastructural characterization of gills in juveniles of the Argentinian silverside, *Odontesthes bonariensis* (Valenciennes, 1835) (Teleostei: Atheriniformes). *Anatomia, Histologia, Embryologia*, *35*, 76–83.

Wilson, J. M., & Laurent, P. (2002). Fish gill morphology: Inside out. *Journal of Experimental Zoology*, *293*, 192–213.

Yashpal, M., Kumari, U., Mittal, S., & Mittal, A. K. (2007). Histochemical characterization of glycoproteins in the buccal epithelium of a catfish *Rita rita*. *Acta Histochemica*, *109*, 285–303.

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