

Morphological description of spontaneous pelvic fin loss in a neotropical cichlid fish

Nicolás Roberto Ehemann¹  | Axel Meyer¹  | Christopher Darrin Hulsey² 

¹Department of Biology, University of Konstanz, Konstanz, Germany

²School of Biology and Environmental Science, University College Dublin, Dublin, Ireland

Correspondence

Christopher Darrin Hulsey, School of Biology and Environmental Science, University College Dublin, Dublin D04 V1W8, Ireland.
Email: darrin.hulsey1@ucd.ie

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Abstract

Pelvic fins are a characteristic structure of the vertebrate Bauplan. Yet, pelvic fin loss has occurred repeatedly across a wide diversity of other lineages of tetrapods and at least 48 times in teleost fishes. This pelvic finless condition is often associated with other morphological features such as body elongation, loss of additional structures, and bilateral asymmetry. However, despite the remarkable diversity in the several thousand cichlid fish species, none of them are characterized by the complete absence of pelvic fins. Here, we examined the musculoskeletal structure and associated bilateral asymmetry in Midas cichlids (*Amphilophus* cf. *citrinellus*) that lost their pelvic fins spontaneously in the laboratory. Due to this apparent mutational loss of the pelvic girdle and fins, the external and internal anatomy are described in a series of “normal” Midas individuals and their pelvic finless sibling tankmates. First, other traits associated with teleost pelvic fin loss, the genetic basis of pelvic fin loss, and the potential for pleiotropic effects of these genes on other traits in teleosts were all reviewed. Using these traits as a guide, we investigated whether other morphological differences were associated with the pelvic girdle/fin loss. The mean values of the masses of muscle of the pectoral fin, fin ray numbers in the unpaired fins, and oral jaw tooth numbers did not differ between the two pelvic fin morphotypes. However, significant differences in meristic values of the paired traits assessed were observed for the same side of the body between morphotypes. Notably, bilateral asymmetry was found exclusively for the posterior lateral line scales. Finally, we found limited evidence of pleiotropic effects, such as lateral line scale numbers and fluctuating asymmetry between the Midas pelvic fin morphotypes. The fast and relatively isolated changes in the Midas cichlids suggest minor but interesting pleiotropic effects could accompany loss of cichlid pelvic fins.

KEYWORDS

fluctuating asymmetry, limb loss, muscles, pleiotropy

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1 | INTRODUCTION

The pelvic fins of teleost fishes and the hind limbs of tetrapods are one of the most evolutionarily conserved and characteristic structures of the vertebrate Bauplan (Don et al., 2013, 2016; Kuznetsov, 2022; Lennox, 2002; Lin et al., 2016; Ogle, 1882; Romer & Parsons, 1986; Starck, 1959, 1979; Yamanoue et al., 2010). However, the paired pelvic appendages have also been lost numerous times in many lineages of tetrapods, as well as in at least 26 of the ~70 extant orders of teleost fishes (Charest et al., 2018; Don et al., 2013; Jackson et al., 2018; Lin et al., 2016; Nelson et al., 2016; Tanaka et al., 2005). In eels, limbless lizards, and snakes, this type of pelvic fin (and pectoral) girdle reduction has permitted extensive organismal diversification into completely new lifestyles (Infante et al., 2018; Jackson et al., 2018; Leal & Cohn, 2018; Pincheira-Donoso et al., 2013; Saxena & Cooper, 2021).

Several Midas cichlid (*Amphilophus* cf. *citrinellus*) species have been maintained in the laboratory for many decades, and loss of the pelvic fins has never been observed previously. However, when an aquarium containing a mixture of Midas cichlids was culled, we observed what we inferred to be a recent loss of the pelvic fins (Figure 1) in a number of these individuals. Therefore, we describe the musculoskeletal changes associated with this pelvic fin loss and examine its potential association with internal and external morphological and meristic changes in other anatomical structures.

The pelvic fins are anatomically and functionally relatively simple and evolutionarily quite malleable in teleosts (Jackson et al., 2018; Standen, 2008; Wicaksono et al., 2016). For instance, the pelvic base in cichlids is formed from only two thickened bony plates fused at their anterior end into a structure known as the basipterygium (Hilton, 2011; Standen, 2017). Like other Acanthomorph teleosts, the pelvic fins in cichlids often have an anterior spine accompanied by several softer fin rays (Barlow, 2002; Nelson et al., 2016; Saemi-Komsari et al., 2018; Figure 2). Usually, the teleost pelvic fin musculature is comprised of six muscles (three analogous muscles lying on each side of the pelvis): two adductors, two abductors, and two arrectors (Siomava & Diogo, 2017; Winterbottom, 1974; Yamanoue et al., 2010). Although these appendages increase maneuverability and control during locomotion (Hilton, 2011), the pelvic fin's influence on powered movement through the aquatic environment has traditionally been considered to be least important among teleost fins (Gosline, 1971; Standen, 2008; Yamanoue et al., 2010). These paired appendages have also been coopted into many other functional structures, such as sucking disks (gobies), walking structures (frogfishes), stationary elements (ipnoids), flying structures (four-wingers), enhanced defensive elements (rockfishes and sticklebacks), brood pouches (ghost pipefishes) and can often be colorful and used in courtship (e.g., cichlids), or as intromittent organs (e.g., poecilids, goodeids, and anablepids) in many teleost lineages (Baldauf et al., 2010; Cole & Ward, 1969; Helfman et al., 2009; Nelson et al., 2016; Salzburger et al., 2007; Yamanoue et al., 2010). The structural simplicity, reduced importance during movement, and frequent cooption into

other functional structures suggest that the pelvic fins might not be highly constrained during teleost evolution.

Although cichlid fishes and many other groups have never completely lost their pelvic fins, the pelvic fins have been lost independently in at least 48 lineages across teleost fishes (Costa et al., 2023; Jackson et al., 2018). Despite many of these lineages having an eel-like body (e.g., Anguilliformes and Saccopharyngiformes), some members of more "typical" percomorph-bodied lineages (e.g., Percopsiformes, Cyprinodontiformes, Perciformes, and Carangiformes), and Siluriformes have also lost their pelvic fin (Costa et al., 2023; Gregory & Conrad, 1937; Jackson et al., 2018; Nelson et al., 2016). Several of these lineages have also evolved characteristic traits that could have changed to compensate for their lack of pelvic fins (Table 1). However, some of these morphological changes could have also been due to the pleiotropic effects of the same underlying genomic changes that led to pelvic fin reduction or loss (Tables 2 and 3, respectively). For example, characteristics such as body elongation, increased number of vertebrae, and the number of remaining pterygiophores could all be pleiotropically modified by genes that also alter pelvic fin anatomy (Ledford & Webb, 2020; McCosker & Ho, 2015; Nelson et al., 2016; Reis & de Pinna, 2019; Tanaka et al., 2005; Zhang et al., 2002). The loss of pelvic fins in many fish groups might be heavily constrained by pleiotropic effects on other anatomical structures.

However, population-level adaptive reduction of the pelvic fins has been inferred to have occurred many times independently, intraspecifically, and rapidly in species such as stickleback fishes (*Gasterosteus aculeatus*, *Pungitius pungitius*, and *Culaea inconstans*) that have lost their pelvic fin numerous times across their large Nearctic distributions (Bell et al., 1993; Chan et al., 2010; Jones et al., 2012; Klepaker et al., 2013; Xie et al., 2019). These convergent losses of pelvic fins have naturally occurred in many recently deglaciated freshwater habitats within the last ~20,000 years (Bell et al., 1993; Elmer & Meyer, 2011; Klepaker et al., 2013; Laurentino et al., 2020; McPhail & Lindsey, 1970; Shapiro et al., 2006). A large proportion of the evolution that takes place when oceanic stickleback invades freshwater ecosystems can happen in less than 50 generations after colonization (Lescak et al., 2015). Interestingly, pelvic fin reductions have also been documented to occur in approximately a dozen generations under experimental conditions (Chan et al., 2010). Similarly, the loss of pelvic fins in genetically modified zebrafish (*Danio rerio*) has also occurred rapidly in the laboratory (Don et al., 2011, 2016; Lin et al., 2016). Pelvic fin loss could be a relatively easy and quick evolutionary transition in many groups of fishes.

Despite the repeated ease with which pelvic fins could be lost in some fishes, losing these fins could substantially affect other anatomical structures. This could commonly constrain the loss of these fins. For instance, several conserved limb genes underlying pelvic fin reduction have been identified (Table 2) that likely influence multiple other anatomical structures (Infante et al., 2018; Lettice et al., 2014; Sagai et al., 2005; Thompson et al., 2018). The genetic basis of pelvic fin loss has previously been shown to occur due to

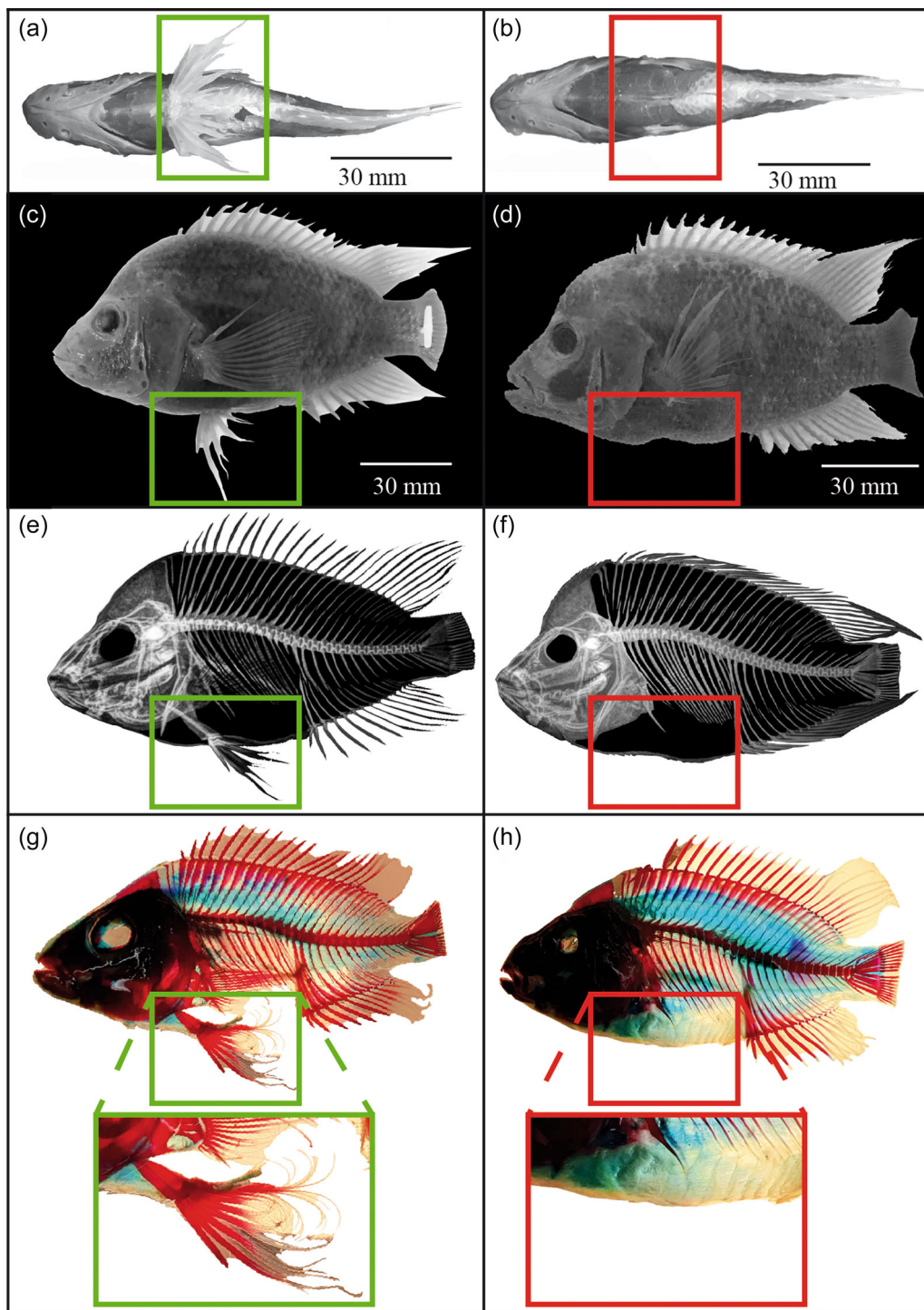


FIGURE 1 Normal (left side) and pelvic finless (right side) morphotypes. The green boxes indicate the location of the pelvic fins in normal individuals, and the red boxes show where the spontaneous appendage loss occurred. Grayscale photograph of the ventral and lateral view (a)–(d). X-ray images showing the osteology of both morphotypes (e) and (f). The basipterygium is evident in the normal morphotype (e); however, it is missing in the pelvic finless specimens (f). The cleared and stained pelvic skeletal structures (g) and their absence in the morphotype without the pelvic fins are shown (h). All photographic backgrounds were digitally removed.

modifications of regulatory genes such as *Hoxd9*, *Pitx1*, *Pitx2*, *Shh*, and *Tbx4* (Chan et al., 2010; Chen et al., 2019; Don et al., 2016; Lin et al., 2016; Marcil et al., 2003; Tanaka et al., 2005; Yamada et al., 2021). These genes are also expressed widely in many other structures during development (Table 3). For instance, *Hoxd9*

influences the positioning of the dorsal, pectoral, and anal fins (Chen et al., 2017a; Mazurais et al., 2009; Tanaka et al., 2005) and *Shh* patterns scales, spines, and teeth (Fraser et al., 2008, 2009; Höch et al., 2021; Hulsey et al., 2019; Sire & Akimenko, 2004). The pleiotropic effect of these genes could provide a guide to investigate

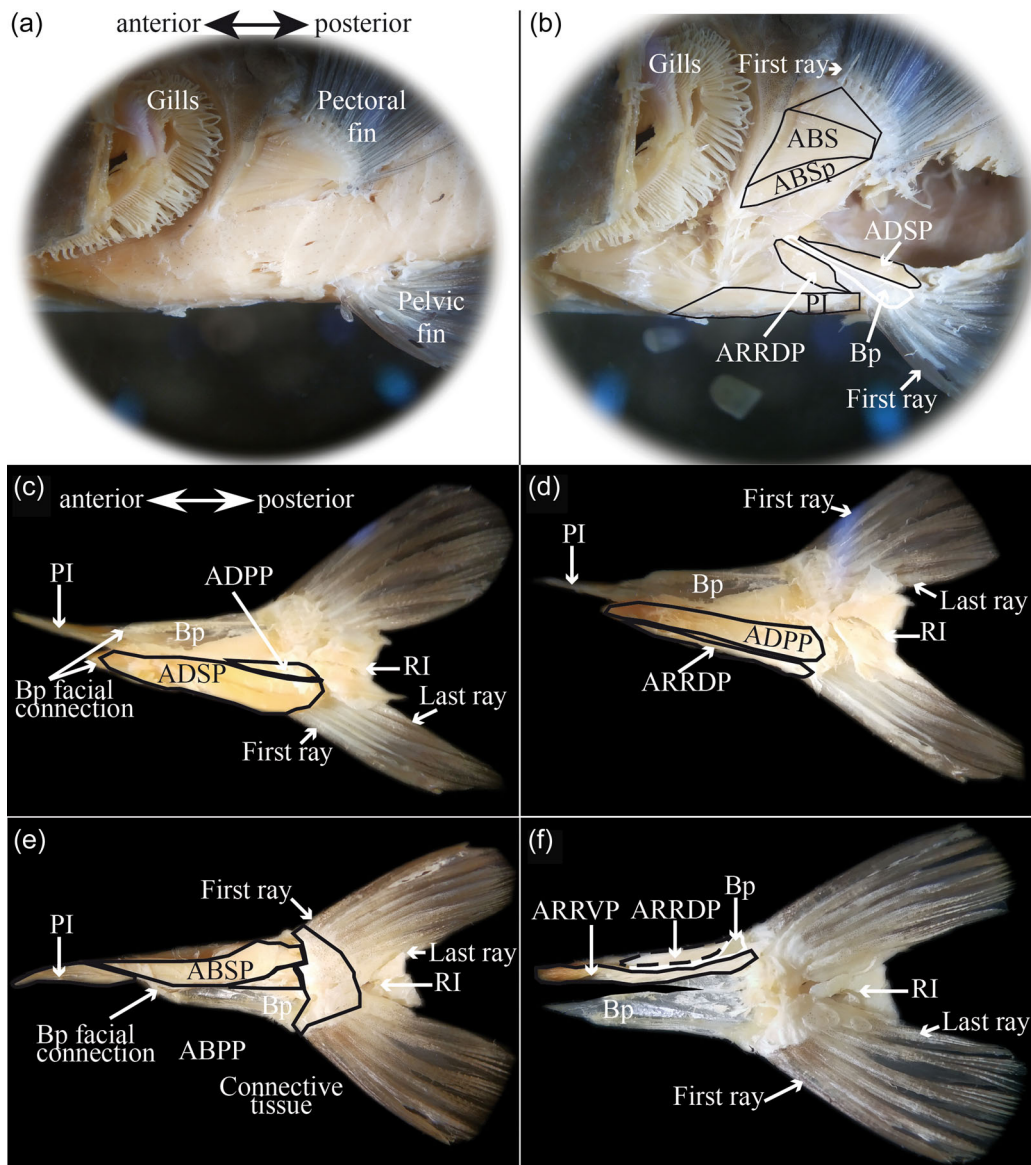


FIGURE 2 Pelvic girdle anatomy in a Midas cichlid. The lateral view of the left pectoral and pelvic fins is shown following removal of scales and skin (a). The exposed pectoral and pelvic muscles are also highlighted after removal of the abdominal muscles (b). The dorsal view of the pelvic girdle musculature is shown once the girdle is removed from the fish (c) and (d). The ventral view of the pelvic girdle musculature is also displayed (e) and (f). The background of the photographs was digitally removed. A subset of the pectoral muscles, the *abductor superficialis* (ABS) and the *abductor superficialis pars profunda* (ABSp) highlight the close proximity of the pectoral fin to the pelvic girdle. The pelvic girdle's basipterygium (Bp) is formed from the fusion of two thickened bony plates. Substantial connective tissue links the pelvic fin rays to the Bp. The eight muscles normally found in the intact pelvic girdle include the *abductor superficialis pelvius* (ABSP), *abductor profundus pelvius* (ABPP), *adductor superficialis pelvius* (ADSP), *adductor profundus pelvius* (ADPP), *arrector dorsalis pelvius* (ARRDP), *arrector ventralis pelvius* (ARRVP), *protactor ischii* (PI), and the *retractor ischii* (RI). Virtually all of this pelvic fin musculoskeletal structure was absent in the pelvic finless Midas cichlids.

other anatomical phenotypes that might change in concert when the pelvic fins are lost.

Pelvic fin loss could also influence the bilateral symmetry of organisms. For instance, the genes *Pitx1* and *Pitx2* that influence pelvic fin loss are also related to deviations from bilateral symmetry in paired structures (Coyle et al., 2007; Graham et al., 2010; Graham, 2021; Gurnett et al., 2008; Marcil et al., 2003; Shapiro et al., 2006). These types of deviations from left versus right lateral

symmetry have been influential in fish evolution, ecology, feeding, reproduction, and locomotion (Campbell et al., 2020; Chapleau, 1993; Kusche et al., 2012; Munroe, 2014; Raffini & Meyer, 2019; Takeuchi & Hori, 2008; Torres-Dowdall et al., 2019). For example, the teleost order Pleuronectiformes (including flounders, turbot, and soles) contains several cases of asymmetry in fishes. After larval metamorphosis, these fish rearrange their eye positions, pigmentation, and paired fin locations (Chen et al., 2017b; Nelson et al., 2016).

TABLE 1 Divergence in morphological traits in teleost fish that have lost their pelvic fins.

Trait	Teleost lineage	Morphological divergence	References
Increased number of vertebrae	Anguilliformes	Up to 220	Huang et al. (2021); McCosker and Ho (2015)
	Syngnathidae	Up to 50	Short and Trnski (2021); Small et al. (2016)
	Pentaacidae	Up to 44	Nelson et al. (2016)
Increased dorsal fin spines and rays	<i>Eumecichthys fiski</i>	Up to 382	Kukuev et al. (2020)
	Gymnarchidae	Up to 230	Hu et al. (2006); Olopade and Taiwo (2013)
Anal fin	<i>Japigny kirschbaum</i>	Decreased fin rays	Meunier et al. (2011)
	Sternopygidae	Increased fin rays	Dutra et al. (2014); Meunier et al. (2014)
Pectoral fins	<i>Trichomycterus aleterus</i>	Decreased	Fernandez and Andreoli-Bize (2017); Ledford and Webb (2020)
	<i>Lucigobius adapel</i>	Decreased fin rays	Okiyama (2001)
	<i>Channa nox</i>	Decreased fin rays	Zhang et al. (2002)
	Giganturidae	Fins high on the body	Johnson (1991)
	<i>Xiphias gladius</i>	Fins low on the body	Gregory and Conrad (1937); Nelson et al. (2016)
	Empetrichthyinae	Wide pectoral base	Nelson et al. (2016)
	Carangidae	Extended rays	Nelson et al. (2016)
Lateral line system	<i>Lucigobius adapel</i>	Decreased lateral line scales	Okiyama (2001)
	Amblyopsidae	Lateral line absent in many cavefish	Poly and Proudlove (2004)
	Cryptacanthodidae	Increased number of cephalic pores	Nelson et al. (2016); Schnell and Hilton (2015)
Teeth	<i>Xiphias gladius</i>	Toothless in adults	Nelson et al. (2016)
	Syngnathidae	Toothless	Nelson et al. (2016); Short and Trnski (2021); Small et al. (2016)

Note: Morphological aspects of these same structures were quantified in the normal and pelvic finless Midas cichlid morphotypes.

However, the pelvic fins in Midas are the last fins to develop during ontogeny (Molina-Arias, 2011), so any genetic changes affecting these structures could have a limited impact on the morphological divergence and symmetry in other structures. Therefore, it is unclear whether the spontaneous loss of pelvic fins we observed in Midas cichlids could have either significant pleiotropic effects on other structures or influence bilateral symmetry in these fishes.

In this study, we anatomically described a spontaneous loss of the pelvic girdle and its associated external fins in a Nicaraguan Midas cichlid reared in our laboratory stocks. The musculoskeletal anatomy and several meristic traits were compared between the two pelvic fin morphotypes to assess whether there were any pleiotropic morphological effects associated with the loss of the pelvic fins. We quantified the number of abdominal as well as the caudal vertebrae, the number of rays in the caudal, dorsal, anal, pectoral, and pelvic fins, the oral teeth in the first row, the cranial sensory pores, the upper lateral line scales, and lower lateral line scales. Lateral asymmetry in both pelvic fin morphotypes was also investigated by measuring the number of pectoral rays, the cranial sensory pores, and the number of upper and lower lateral line scales on both the left and right sides of the fish. Using these anatomical measurements, we

determined how the spontaneous loss of the pelvic appendages might have pleiotropically influenced other Midas cichlid musculoskeletal structures as well as external left-right asymmetry.

2 | MATERIALS AND METHODS

2.1 | Midas cichlid fish specimens

All 67 Midas cichlids specimens (*A. citrinellus*) used were young adult size. Of these, 29 had the pelvic fins and girdle (Figure 1), what we termed the “normal” morphotype ranging between 80.2 and 130.2 ($\bar{x} = 94.9 \pm 11.7$) mm standard length (SL). Meanwhile, 38 lacked these pelvic structures, what we termed the “pelvic finless” morphotype (Figure 1), and spanned a range of 60.7–140.7 ($\bar{x} = 105.0 \pm 17.4$) mm SL. All of the fish were siblings and were initially housed in the same aquarium. These fish were obtained from an aquarium population recently culled by animal care technicians (~1 week prior). The loss of the pelvic fins went undetected for the first year of their lives as these fish grew. These were fed daily, and no obvious disadvantages in swimming ability were observed between the pelvic

finless morphotypes and their normal siblings. Additionally, since the groups did not differ in their body sizes, it seems both groups increased in length equally well. Once discovered, a series of both

pelvic fin morphotypes were preserved in 70% ethanol (EtOH) for long-term storage.

TABLE 2 Genes associated with pelvic fin absence (A) and reduction (R) in different fish species.

Gene	Species	Reference(s)
<i>Hoxd9</i>	<i>Takifugu rubripes</i> (A)	Tanaka et al. (2005)
	<i>Dicentrarchus labrax</i> (A/R)	Mazurais et al. (2009)
<i>Pitx1</i>	<i>Gasterosteus acuelatus</i> (A/R)	Chan et al. (2010); Cole et al. (2003); Coyle et al. (2007); Shapiro et al. (2006); Thompson et al. (2018)
	<i>Pungitius pungitius</i> (A/R)	Shapiro et al. (2006)
<i>Pitx2</i>	<i>Gasterosteus acuelatus</i> (A/R)	Cole et al. (2003)
<i>Shh</i>	<i>Danio rerio</i> (R)	Letelier et al. (2018)
	<i>Oryzias latipes</i> (R)	Letelier et al. (2018)
<i>Tbx4</i>	<i>Danio rerio</i> (A)	Cole et al. (2003); Don et al. (2016); Lin et al. (2016)
	<i>Syngnathus</i> spp. (A)	Lin et al. (2016); Small et al. (2016)
	<i>Hippocampus</i> spp. (A)	Lin et al. (2016)
	<i>Corythoichthys</i> sp. (A)	Lin et al. (2016)
	<i>Anguilla japonica</i> (A)	Chen et al. (2019)
	<i>Takifugu</i> spp. (A)	Chen et al. (2019)
	<i>Tetraodon nigroviridis</i> (A)	Chen et al. (2019)
	<i>Pampus argenteus</i> (A)	Zhang, Zhang, et al. (2022)

2.2 | Pelvic and pectoral fin osteology and muscles

To examine the internal calcified structures of the fishes, X-ray plates were produced using a ZooMax Digital X-ray machine set at values of 52 kV peak and 4–7 mAs. X-rays were obtained from the lateral view of 40 specimens ($n = 20$ normal; $n = 20$ pelvic finless). The pelvic morphotype was confirmed based on the presence of the basiptyrgium. Additionally, the pelvic fin musculature presence and absence was examined in both morphotypes. The distal and proximal insertion of the *arrector ventralis pelvificus* (ARRVP), *arrector dorsalis pelvificus* (ARRDP), *abductor superficialis pelvificus* (ABSP), *abductor profundus pelvificus* (ABPP), *adductor superficialis pelvificus* (ADSP), *adductor profundus pelvificus* (ADPP) *protactor ischii* (PI), and *retractor ischii* (RI) (Figure 2) were examined following Winterbottom (1974) and Siomava and Diogo (2017).

The X-ray images were also used to investigate any pleiotropic effects on vertebrae numbers. To quantify vertebrae numbers, both the abdominal (vertebrae bearing ribs) and caudal vertebrae (with hemal spine), according to Nikiforidou et al. (2020) were counted. In addition, the X-ray images allowed us to count the proximal pterygiophores of the dorsal, anal, and caudal fins of each specimen.

As we initially hypothesized that the loss of the pelvic fins might influence the pectoral fin morphology, the right pectoral girdle and fin of 20 specimens ($n = 10$ normal; $n = 10$ pelvic finless) were carefully removed from the fish. Under a dissection microscope and using forceps and a scalpel, these fins were detached from the body at the supracleithrum and postacleithrum joints. Then, each muscle was

TABLE 3 Anatomical structures associated with genes linked to pelvic fin absence or reduction in fish.

Pleiotropic structures	Species	Gene(s)	References
Scales	<i>Danio rerio</i>	<i>Shh</i>	Sire and Akimenko (2004)
	<i>Danio rerio</i>	<i>Tbx</i> cluster	Zhang, Ji, et al. (2022)
Teeth	<i>Syngnathus scovelli</i>	<i>Pitx1</i>	Small et al. (2016)
	Malawi Cichlid species	<i>Hox</i> , <i>Pitx2</i> , <i>Shh</i>	Fraser et al. (2008, 2009)
	<i>Danio rerio</i>	<i>Pitx2</i>	Square et al. (2021)
	<i>Gasterosteus acuelatus</i>	<i>Pitx2</i>	Square et al. (2021)
Pectoral fin	<i>G. acuelatus</i> , <i>Takifugu rubripes</i>	<i>Hoxd9</i>	Tanaka et al. (2005)
	<i>Danio rerio</i> , <i>Oryzias latipes</i>	<i>Shh</i>	Letelier et al. (2018)
Dorsal and anal spines	<i>Paralichthys olivaceus</i>	<i>Hoxd9</i>	Chen et al. (2017a)
	<i>Pelteobagrus fulvidraco</i>	<i>Tbx4</i>	Chen et al. (2019)
	Scorpaeniformes	<i>Tbx4</i>	Chen et al. (2019)
Spiny and soft rays	<i>Astatotilapia burtoni</i>	<i>Shh</i>	Höch et al. (2021)
Ribs	<i>Syngnathus scovelli</i>	<i>Hox</i> , <i>Pitx</i> , <i>Tbx</i>	Small et al. (2016)

Note: These candidate structures that potentially could have been modified were examined in our two Midas cichlid pelvic fin morphotypes.

dissected following Winterbottom (1974), Thorsen and Westneat (2005), Standen (2010), and Hulseley et al. (2013). The *abductor superficialis* (ABS), *abductor superficialis pars profunda* (ABSp), *arrector ventralis* (ARRV), and *abductor profundus* (ABP) that all pull the fin anteriorly were first carefully separated and removed from the pectoral girdle. Then, the *arrector dorsalis* (ARRD), *adductor radialis* (ADR), *adductor profundus* (ADP), and *adductor superficialis* (ADS) that pull the pectoral fin posteriorly were removed. Finally, each dissected muscle was blotted dry twice on paper towels and subsequently weighed (± 0.0001 g). We then calculated the percentage of the mass of each individual pectoral muscle that contributed to the combined total pectoral muscle mass to determine if there were differences in individual pectoral muscle masses between the pelvic finless and normal morphotypes.

2.3 | Skeletal clearing and staining

Due to the limited ability of X-rays to capture changes in less calcified structures (e.g., cartilage), particularly in the pelvic fins, two specimens of each morphotype were also cleared and stained. Alcian blue and alizarin red staining was employed, according to Dingerkus and Uhler (1977) and Potthoff (1984). In brief, specimens were fixed in 7% formalin for approximately 1 week. After several washes with deionized water, the samples were postfixed in 70% EtOH for at least 72 h. Next, the cartilage structures of the specimens were stained using 20 mg of alcian blue diluted in 30% glacial acetic acid (HAc) and 70% pure EtOH for 6–8 h. Then, the fish were placed in an EtOH/HAc wash for 1 h and transferred to 70% EtOH and water for 24 h. Next, specimens were put into a solution of 1% pork pancreas trypsin 1:250 (Genaxxon Bioscience) and 30% saturated sodium borate until the blue-stained cartilages were visible. Specimens were then transferred to distilled water with 2–5 drops of 30% hydrogen peroxide for at least 24 h. Subsequently, calcified fish structures were stained using alizarin red dissolved in 0.5% potassium hydroxide (KOH) solution for 24 h and transferred to a 0.5% KOH solution for 1 day. After several washes with a 0.5% KOH solution, fish were gradually transferred to 100% glycerol for final storage. All dissections and visualization in this study were performed under a ZEISS Stemi SV 11 stereoscope and photographed with a Zeiss AxioCam MRc camera.

2.4 | Morphometric and meristic data

To quantify the external anatomy, morphometric analyses of selected traits were performed on the left side of all specimens. Three measurements were taken using an analog caliper (± 0.1 mm). These measurements were the SL from the snout to the tail-end of the vertebral column, the pectoral fin base height estimated at the cartilage pad section, and the pectoral fin length from the origin of the fin to the tip of the longest ray. These data were size-standardized as a percentage of the SL for statistical analyses. The

number of teeth in the first row of the upper and lower jaw was also quantified from the left side of 20 individuals of each morphotype. When present, the paired pectoral and pelvic fin rays were counted on both fins. In addition, the pores running along the anterior lateral line system, particularly on the mandibular-preopercular and the infraorbital canal, were counted on both sides of the fish (Edgley & Genner, 2019). As cichlids have a divided posterior lateral line (Nelson et al., 2016; Recknagel et al., 2013; Scott et al., 2023), both the upper and lower lateral line scales were counted for all specimens on the right as well as the left sides of the fish.

Finally, we evaluated the degree of asymmetry between the Midas pelvic fin morphotypes for several traits: (1) pectoral ray fins, (2) mandibular-preopercular canal pores, (3) infraorbital canal pores, (4) upper lateral line scales, and (5) lower lateral line scales. Paired test comparisons were performed on the meristic values for the same side of the body between the morphotypes. To quantify if the degree of asymmetry differed between the two morphotypes, we followed the methodology suggested by Graham (2021), Graham et al. (2010), and Palmer and Strobeck (1986). In brief, the value of d ($d = \text{left} - \text{right}$) was estimated for each specimen and assessed by subtracting the meristic values of the left side and the value of its right. Then, E was estimated ($E = |d - 0|$). This absolute value was used to compare the extent of asymmetry in the two pelvic fin morphotypes with a paired test. Normality and homogeneity of variance assumptions were assessed using Shapiro and Leven's tests, respectively. Based on the results, paired t-tests or Wilcoxon rank-sum tests were selected for the comparisons. Statistical analyses were performed using the software PAST version 4.09 (Hammer et al., 2001).

3 | RESULTS

The presence and absence of the external pelvic girdle structures were clearly evident in both morphotypes after removing the scales and skin (Figure 1). The *protactor ischii* tendon located along the ventral midline was thicker in the normal specimens compared to the pelvic finless individuals (Figure 1a,b). Additionally, muscle striations of the *protactor* and *retractor ischii* could not be histologically or visually confirmed in the pelvic finless individuals. Therefore, any homology of this thin membrane to these putative muscles is tenuous. The pelvic fins and the basipterygium that inserts anteriorly near the cleithrum of the pectoral fin were clearly evident in the normal morphotype and absent in the pelvic finless group (Figure 1c–h). Remarkably, there was no evidence of either a calcified (Figure 1f) or cartilaginous (Figure 1h) basipterygium in the specimens with the pelvic finless morphotype. Furthermore, the pelvic muscles comprising the ABSP, ABPP, ARRVP, ADSP, ADPP, ARRD, PI, and RI were present exclusively in the Midas retaining their pelvic fins (Figure 2).

All normal and pelvic finless X-rayed specimens showed a similar arrangement of calcified structures for the pectoral girdle (Figure 1e,f), and this was also evident in cleared and stained

specimens (Figure 1g,h). Additionally, no differences were observed among the configuration of the bones making up the pectoral girdle. The cleithrum, scapula, coracoid, and four radials contributing to the pectoral fin were consistently present in both morphotypes. Furthermore, the eight muscles dissected from the pectoral girdle comprised a similar proportion of the total muscle mass (Figure 3a,b), and the same layout of each of these muscles (Figure 3c–f) was observed in the two morphotypes. The total mass of the pectoral fin *abductor* (48.4% and 47.5%), *adductor* (40.1% and 40.0%), and the *arrector* (11.5% and 12.5%) muscles were broadly similar between the normal and the pelvic finless morphotypes. The group lacking the pelvic fins had slightly higher proportions for the ABP, ARR, ADP, and ARRD (Figure 3a,b). However, these were not significantly different ($p > .05$) from the normal morphotype (Table S1).

The morphometrics of most traits were generally similar between the two pelvic fin morphotypes. After size-standardization, the pectoral base height was slightly higher in the pelvic finless morphotype ($p < .05$). However, no differences were observed in the pectoral fin length between the two groups. The meristic data were also generally similar between the Midas pelvic fin morphotypes (Table 4). The numbers of rays in the caudal (22) and dorsal fin (27), as well as the numbers of the upper first row of teeth (15), were equivalent and invariable between the pelvic fin morphotypes (Table 4). Some differences in the anal ray counts, first-row teeth in the lower jaw, and vertebrae were found (Table 4), although none differed substantially between the two morphotypes. For example, three individuals of each morphotype had 15 anal fin rays, and one pelvic finless individual had 13 anal fin rays. Additionally, except for one normal specimen that had 13 abdominal vertebrae instead of 14, similar meristic variation in the total vertebrae for both morphotypes was recovered in the caudal vertebrae. In the normal morphotype, 14 ($n = 1$) and 15 ($n = 6$) caudal vertebrae were present instead of the similarly common 16 ($n = 13$) vertebrae. Eight pelvic finless individuals had 15 caudal vertebrae instead of the more frequent 16 ($n = 12$). The range in the right side first row of teeth in the lower jaw (20–22) was similar between both morphotypes (Table 4).

The meristics of the structures assessed on both the right and left sides of all 67 specimens generally overlapped between the morphotypes but showed interesting patterns. The range in the number of pectoral fin rays (15–17), mandibular-preopercular (8–10), and infraorbital pores canals (3–7) were comparable between the two morphotypes. Yet, the number of pores along the infraorbital canal differed significantly ($p < .05$) between the pelvic fin morphotypes on the left side (Table 5). Additionally, the upper lateral line scale numbers ranged extensively from 0 to 28, and the lower lateral line scales ranged from 0 to 10 (Table 5). Compared to the normal morphotype, the pelvic finless group had higher mean values for five traits on the right side and four traits on the left side of the body (Figure 4 and Table 5). In terms of mean values, a left-right asymmetry dominance where higher values on the left side than the right was observed regardless of the morphotype (Table 5). Differences in the asymmetry metric E between the morphotypes were found only for the lower lateral line scales (Table 5). However,

the average number of scales along the upper lateral line differed substantially ($p < .05$) between the pelvic fin morphotypes on both the left and right sides of the body (Table 5).

4 | DISCUSSION

The spontaneous loss of the pelvic girdle and associated fins in lab-raised Midas cichlids had pleiotropic effects on the morphology of other structures and the bilateral symmetry of these Midas cichlids. As far as we know, a single cichlid species has been recorded as occasionally lacking a pelvic fin in the wild (Ugbomeh et al., 2022), although similar spontaneous anomalies in the pelvic fin have been reported in wild-caught fishes in many other teleost families such as Blenniidae, Engraulidae, Lutjanidae, and Nemipteridae (Alvarez-León, 1980; Babu-Rao, 1975; Hettler, 1971; Jawad et al., 2017, 2022; Jose et al., 2020; Marr, 1945; Menezes, 1961). However, these other studies generally lack detailed comparative morphological analyses between fish with and without pelvic fins. The pleiotropic morphological consequences of the loss of structures like the pelvic fin should be examined more extensively as they could point to reasons outside the functional consequences of pelvic fin loss that could help to maintain the evolutionary retention of these paired appendages.

The causes of many pelvic fin anomalies in teleosts are still unclear. Frequently, similar biotic (e.g., genetic and poor nutrition), abiotic (e.g., temperature, pollution, and oxygen), or a combination of both factors have been hypothesized to cause these types of anatomical anomalies (e.g., Bengt-Erik et al., 1985; Ehemann et al., 2022; Eissa et al., 2021; Gudger, 1930; and Jawad & Ibrahim, 2018). Additionally, the loss of the pelvic fins defines many diverse fish lineages, where ecological conditions (e.g., lack of predators in stickleback freshwater population) may facilitate or even drive the loss of “unnecessary” fins. The rapid and spontaneous loss of the pelvic fins in the Midas assessed in this study is unlikely to be explained by adaptation to abiotic or biotic factors because both Midas morphotypes were siblings and tankmates and reared under the same constant conditions. However, the observed loss in aquaria and its influence on other morphological structures could provide novel insights into why pelvic fin loss might be uncommon in cichlids and perhaps other fishes.

The genetic causes of pelvic fin loss or reduction in many fishes continue to become apparent (Table 2). Our findings support the growing evidence that pelvic fin loss can occur rapidly (Bell et al., 1993; Chan et al., 2010; Don et al., 2016; Kratochwil & Meyer, 2019) and might frequently have a relatively simple genetic basis (Table 2). The meristic variation in many of the morphological traits examined (Tables 4 and 5) was similar to normal patterns of variation observed in other fishes (Tables 1–3). For instance, there was some variation in traits, such as the number of caudal vertebrae that commonly show minor variation in fishes (Losada et al., 2014; Reyes-Corral & Aguirre, 2019). However, the differences found with the number of lateral line scales, not only between the morphotypes but also between sides of the body, suggest that the loss of the pelvic

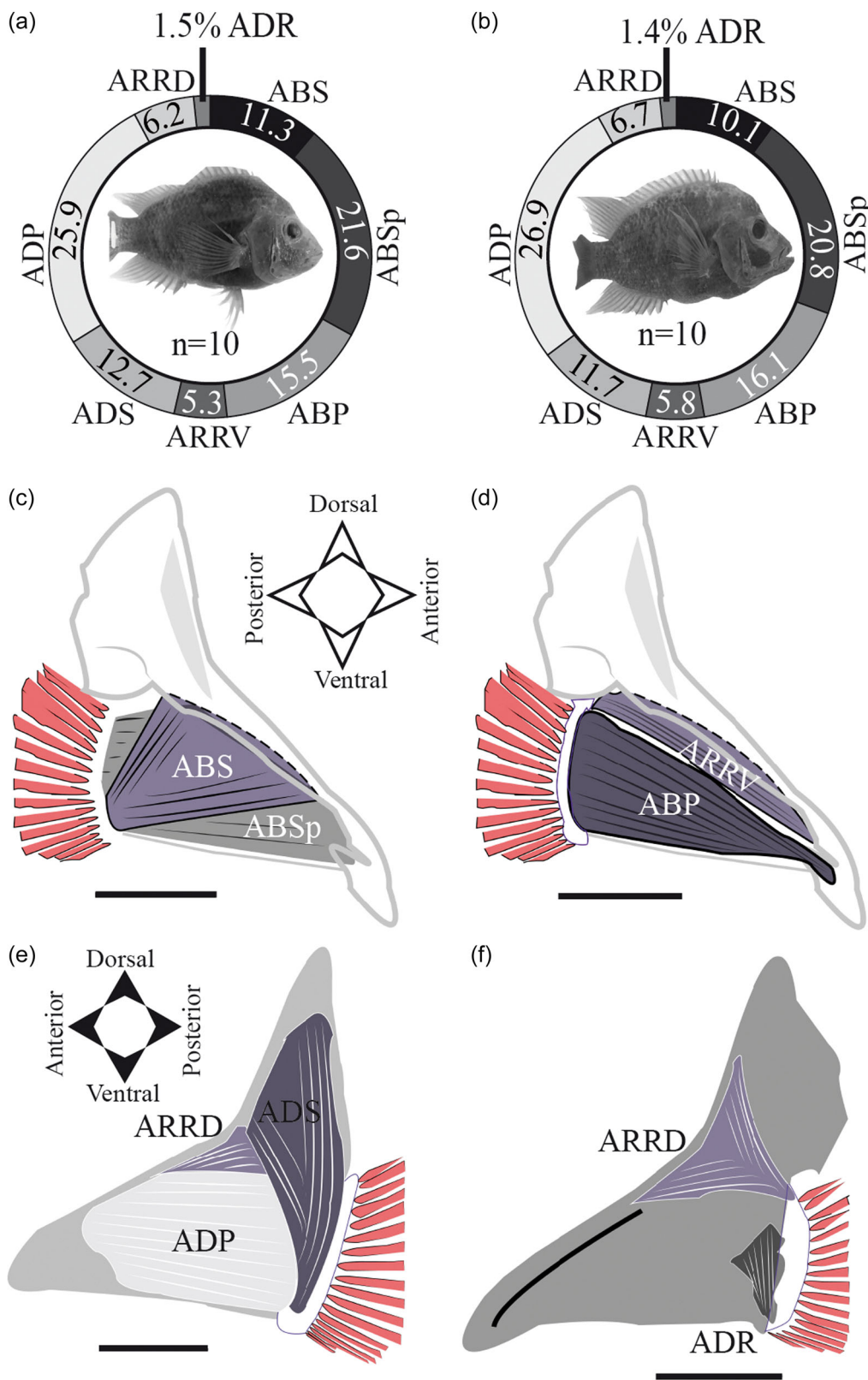


FIGURE 3 Individual percentage contribution (summarizing total right pectoral weight) of the muscles assessed in this study for the normal (a) and pelvic finless (b) groups. General schematic origins, shape, and insertions of the *abductor superficialis* (ABS), *abductor superficialis pars profunda* (ABSp), *abductor profundus* (ABP), and *arrector ventralis* (ARRV) on the medial external view (c) and (d). The *adductor superficialis* (ADS), *adductor profundus* (ABP), *arrector dorsalis* (ARRD), and *adductor radialis* (ADR) are located on the inner side of the pectoral girdle (e) and (f).

TABLE 4 Meristic comparisons of the unpaired morphological traits gathered from the 20 normal and 20 pelvic finless individuals of *Midas* cichlids.

Morphotype	Normal	Pelvic finless
Variable	Range (mean)	Range (mean)
Abdominal vertebrae	13–14 (13.9)	14–14 (14.0)
Caudal vertebrae	14–16 (15.6)	15–16 (15.6)
Total vertebrae	28–30 (29.5)	29–30 (29.6)
Caudal fin rays	22 (22.0)	22 (22.0)
Dorsal fin rays	27 (27.0)	27 (27.0)
Anal fin rays	14–15 (14.2)	13–15 (14.2)
First row teeth lower right jaw	20–22 (21.4)	20–22 (21.4)
First row teeth upper right jaw	15 (15.0)	15 (15.0)

Note: Range and mean (within parenthesis).

fin could have substantial consequences for other morphological structures. Our results highlight a potential genetic association between the pelvic fins and the lateral line system in fishes whose mechanistic relationship should be examined more extensively.

The limited morphological or meristic differences between the two *Midas* pelvic fin morphotypes in a number of structures (Tables 4 and 5) could be explained by the general timing of pelvic fin development (Woltering et al., 2018). The pelvic fins are the last fin to arise during development in *A. citrinellus*, with the first rays starting to form 17 days after fertilization (Molina-Arias, 2011). Interestingly, *A. citrinellus* also shows a slightly slower larval development rate than other relatively closely related Central American cichlids species, such as *Amatitlania nigrofasciatum*, *Parachromis managuensis*, *Parachromis dovii*, and *Herotilapia multispinosa* (Molina-Arias, 2011). If this slower development especially affects the pelvic fins, this could restrict the probability of pleiotropic effects on either musculo-skeletal structures or organ systems. However, heterochronic

TABLE 5 Left and right-side comparisons of the paired structures between the normal ($n = 29$) and the pelvic finless ($n = 38$) *Midas* cichlids.

Morphotype	Left side		Right side		Asymmetry (E)	
	Normal	Pelvic finless	Normal	Pelvic finless	Normal	Pelvic finless
PR	15.9 ± 0.1	16.1 ± 0.0	15.9 ± 0.1^{w*}	16.1 ± 0.0^{w*}	0.0 ± 0.0	0.1 ± 0.0
MPC	9.4 ± 0.1	9.3 ± 0.1	9.3 ± 0.1^{w*}	9.7 ± 0.1^{w*}	0.3 ± 0.1	0.4 ± 0.1
ICP	5.5 ± 0.1^{wt**}	5.9 ± 0.1^{wt**}	5.7 ± 0.1	5.7 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
ULL	14.1 ± 1.0^{wt*}	17.2 ± 0.6^{wt*}	9.1 ± 0.7^{t**}	12.9 ± 0.8^{t**}	5.8 ± 1.0	5.3 ± 0.6
LLL	6.4 ± 0.6	7.7 ± 0.3	3.5 ± 0.6^{wt***}	6.7 ± 0.4^{wt***}	3.7 ± 0.6*	1.5 ± 0.3*

Note: Values for the pectoral rays (PR), mandibular-preopercular canal pores (MPC), infraorbital canal pores (ICP), upper lateral line scales (ULL), and lower lateral line scales (LLL) are given as mean and stand error for both the left and right sides of each pelvic fin morphotypes. Absolute asymmetry values (E), interpreted as zero for perfect symmetry, were calculated for traits in each of the two pelvic fin morphotypes, and these values between the morphotypes were compared with a parametric t test (t) or alternatively with the nonparametric Wilcoxon rank-sum test (w) to determine if one of the morphotypes showed evidence of more asymmetry. Welch's t test (wt) was used in case of unequal variance (Levene's test $p < .05$). Significant differences are marked in bold font and denoted with asterisks for $p < .05$ (*), $p < .005$ (**), and $p < .0005$ (***).

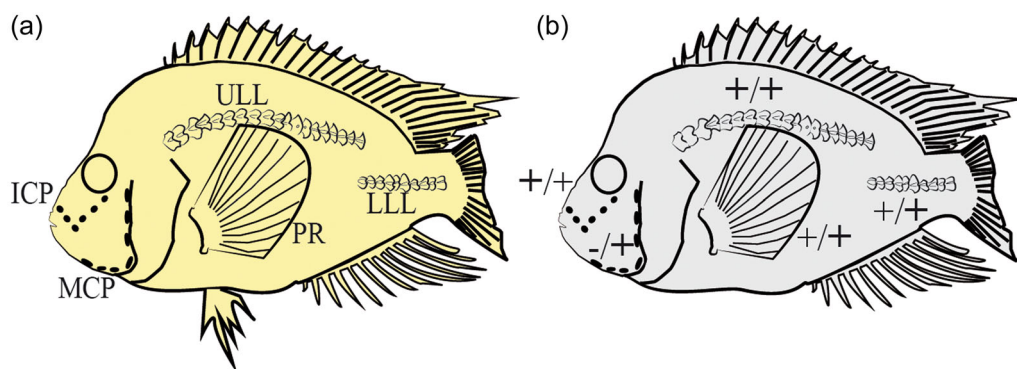


FIGURE 4 Schematic representation of the meristic variables evaluated on both sides of the normal (a) and pelvic finless (b) morphotypes. The pectoral rays (PR), mandibular preopercular canal pores (MCP), infraorbital canal pores (ICP), upper lateral line scales (ULL), and lower lateral line scales (LLL) are depicted. The pelvic finless drawing shows the traits where the meristic mean values were greater (+) or less (-) for each side of the body (left/right) as compared to the meristics in the normal morphotype (b). Statistical differences ($p < .05$) are shown in larger and bold font size.

changes, atavism, and vestiges of pelvic girdles in some other animals (e.g., snakes and whales) have also been found (Hall, 2010; Lanzetti et al., 2023; Sherratt et al., 2019; Stiasny, 1991; Werneburg & Sánchez-Villagra, 2015), and suggest that the timing of pelvic fin development can play a role in their loss. It might be that structures that form later in development are often the ones that are more readily lost during evolution and are also those traits that commonly show limited pleiotropic effects on other anatomy.

The loss of the pelvic fins in the Midas cichlid individuals was accompanied by substantial left-right asymmetry in the pelvic finless morphotype. Interestingly, regardless of the morphotype examined, higher meristic values tended to be found on the left than on the right side when asymmetry was detected (Table 5). Similar results with left dominant asymmetry have also been mentioned for other fish such as stickleback, four-eyed fish, zebrafish and also in other taxa like Cephalochordates, Urochordates, and manatees (Bell et al., 1985; Boorman & Shimeld, 2002; Hamada, 2020; Lajus et al., 2019; Parenti, 1986; Reimchen & Bergstrom, 2009; Řežucha & Reichard, 2015; Seixas et al., 2021; Shapiro et al., 2006; Sinha & Tilak, 1968; Torres-Dowdall et al., 2019, 2022; Yasui et al., 2000). These situations, where body structures on one side (left) are larger for meristic counts than counts on the other side (right), also called left-right asymmetry, have been found to be related to genes such as *Pitx1* (Shapiro et al., 2006) as well as the *Nodal-Pitx2* pathway (Hamada, 2020; Schreiber, 2013; Table 2). The extent of asymmetry was considerably higher for the upper and lower lateral lines for both morphotypes as compared to other traits. The variation observed in the meristics of the lateral line in these cichlids suggests the mechanistic links between the pelvic fin and lateral line morphology should be investigated more extensively in Midas cichlids and other fish lineages. Future research into the shared developmental genetic basis of paired appendages and other structures would help to shed light on the commonalities structuring morphological divergence among the many disparate lineages that have lost their pelvic fins.

5 | CONCLUSIONS

The loss of the pelvic appendages resulted in changes in the musculoskeletal morphology and left-right asymmetry between normal and pelvic finless Nicaraguan Midas cichlid fishes reared in captivity. A comparative review of the anatomy and genes associated with pelvic fin loss in other teleost fishes pointed to several morphological traits that might also differ in association with the loss of the pelvic fins. By examining these potential pleiotropic phenotypes that could change in conjunction with pelvic fin loss, we were able to find several morphometric differences between the two Midas cichlid pelvic fin morphotypes. The morphotypes did differ in meristic traits, such as the fin rays, head pore canals, and lateral line scales. We also observed left-right asymmetry in the number of lateral line scales in both morphotypes. The anatomical differences in the lateral line system suggest a possible developmental and/or other mechanistic link between the pelvic fin and the lateral line system

that should be investigated both within a developmental genetic context as well as with comparative anatomy in other teleost fishes.

AUTHOR CONTRIBUTIONS

All three authors conceptualized the study. Nicolás Roberto Ehemann collected the data and conducted the statistical analyses. Christopher Darrin Hulsey helped to draft the initial manuscript. Nicolás Roberto Ehemann, Axel Meyer, and Christopher Darrin Hulsey all contributed to the editing and writing of the final version of the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data will be submitted to Dryad upon acceptance.

ORCID

Nicolás Roberto Ehemann  <http://orcid.org/0000-0003-1259-1779>

Axel Meyer  <http://orcid.org/0000-0002-0888-8193>

Christopher Darrin Hulsey  <https://orcid.org/0000-0002-9653-6728>

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