



Ecomorphological diversification of the *Cyprinodon* species complex from Lake Chichankanab, Yucatan, Mexico

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Abstract

Chichankanab is a small, shallow, ~8,000-year-old, tropical lake where the adaptive radiation of seven sympatric *Cyprinodon* species have been described. Since the variation in size, morphology, and diet play a key role in facilitating niche partitioning, this study aims to determine if the sympatric species can be independently identified by their variation in size, morphology, and diet and to understand the role of those variables in the ongoing diversification. To fulfill our aim we gathered, from fish collections, an updated sample of the seven sympatric species and the sister species *Cyprinodon artifrons* from whom we took their size and photographs to develop geometric morphometric analyses, and collected information on their diet. According to our results, size range allows the separation of *Cyprinodon beltrani* as the largest species, geometric morphometric allows the segregation *C. beltrani*, *Cyprinodon simus*, *Cyprinodon suaviium*, and *Cyprinodon labiosus*, and a morphotype of three species, *Cyprinodon esconditus*, *Cyprinodon verecundus*, and *Cyprinodon maya*, which can be segregated by body measurements and the size of the species. The diet can help to segregate *C. beltrani* herbivore, *C. maya* piscivore/omnivore, *C. simus* zooplanktivore/detritivore, *C. suaviium* and *C. verecundus* carnivore/molluscivore, and *C. esconditus* and *C. labiosus* carnivores. The ongoing hybridization and the changes in the lake are driving the diversification and decrease of these species. According to our results, there is not one character that differentiated all the species, differentiation was only possible through their specific variation in one character or by a specific combination of characters. It is important to monitor and keep updating information on these evolving species since all seven are listed in the IUCN as vulnerable and near threatened, and according to official Mexican categories as in danger of extinction.

Keywords *Cyprinodon* · Adaptive radiation · Yucatan Peninsula · Morphology · Geometric morphometrics

Introduction

The paleogeographic development of the Yucatan Peninsula shaped its current diversity of ichthyofauna. The eastern coast was especially affected by eustatic changes, which favor the formation of coastal lakes that separate from the sea over time and become inland lakes, as is the case of the Chichankanab (Wilkens 1982). This small (~20 km

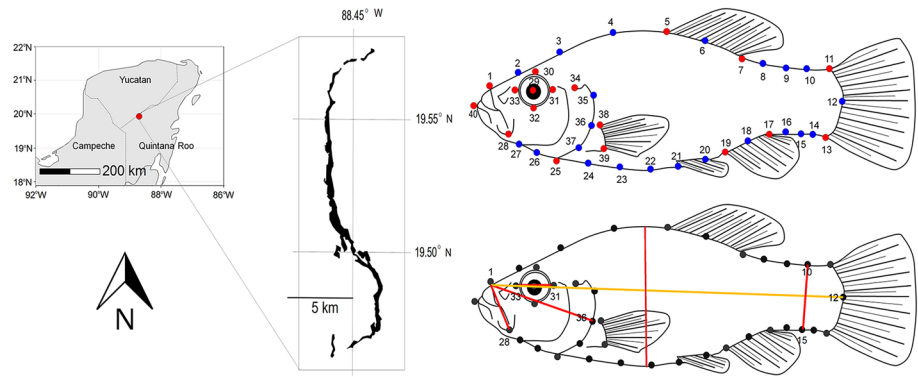
long), shallow, tropical lake is the largest inland body of water in the Yucatan Peninsula (Covich and Stuiver 1974; Hodell et al. 1995; Ramsar 2004). It is a body of freshwater saturated with calcium sulfate (average salinity of 2.4 g/l; Strecker 2006b), where the invertebrate and fish fauna is low in diversity because the water saturated with calcium sulfate it is intolerable to most species (Humphries and Miller 1981; Strecker et al. 1996; Strecker 2006a). However, paleontological studies indicate that when it was first filled about 8,200 years ago it had high concentrations of sulfates and salinity ~13–40 g/l (Humphries and Miller 1981; Strecker 2006b; Perry et al. 2002; Brenner et al. 2003). The climate in the region is warm sub-humid with summer rains, total annual precipitation of 1,100–1,200 mm, and an average annual temperature of 26–28 °C (Ramsar 2004). It is located at the eastern end of the Sierra de Ticul and is presumably the result of the same fault system that produced those mountain ranges (Humphries and Miller 1981; Fig. 1).

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Fig. 1 Left: Chichankanab lagoon and its position (red dot) in the Yucatan Peninsula, Mexico. Right: methods used to quantify the morphological variation of the *Cyprinodon* species from Chichankanab lagoon and *C. artifrons*; top right: geometric morphometric protocol of landmarks (red dots) and semilandmarks (blue dots); bottom right: five body measurements (red lines) and the standard length (yellow line)



Cyprinodon species are mainly known for their isolation in desert hot springs throughout the southwestern United States and Mexico (Miller 1948; Miller et al. 2005). However, in Chichankanab the adaptive radiation of seven monophyletic sympatric *Cyprinodon* species has been described (Humphries and Miller 1981; Humphries 1984a; Strecker 2002, 2005). In adaptive radiations, two main factors seem to play an important role, selective mating, which leads to reproductive isolation (Strecker and Kodric-Brown 1999; Cruz et al. 2004; Boughman et al. 2005), and morphological differentiation which allows the differential use of the resources and habitat choice (Feulner et al. 2007).

It has been indicated that *Cyprinodon* species from Chichankanab evolve isolated from predators and competitors (Fuselier 2001) and show differences mainly in the head morphology, suggesting trophic divergence and the exploitation of different feeding niches (Stevenson 1992). Some of the morphological characters that help to distinguish the species are, *Cyprinodon beltrani* is a deep-bodied species, morphologically similar to *Cyprinodon artifrons* the sister species of the group; *Cyprinodon maya* is the largest species with the larger mouth opening; *Cyprinodon labiosus* present protuberant fleshy lips and an elongate body; *Cyprinodon simus* has a vertical lower jaw, larger eye size, and is the smallest species; *Cyprinodon verecundus* presents a broad mouth opening, large fins, and large eyes; *Cyprinodon esconditus* has broad mouth opening and smaller eye; and *Cyprinodon suaviium* presents terminal mouth with thickened lips (Humphries and Miller 1981; Humphries 1984a; Strecker 2002, 2005).

Despite this morphological variation, different studies have indicated an incipient species partitioning. Trophic studies have shown 40% to over 95% niche overlap among species (Horstkotte and Strecker 2005); laboratory crossings reveal that all species are interfertile (Strecker and Kodric-Brown 1999, 2000; Kodric-Brown and Strecker 2001); and genetic analyses have indicated significant genetic differentiation only for *C. maya* (Strecker 2006a). It has been suggested that this incipient partitioning may result from

speciation proceeded by ongoing hybridization (Humphries 1984b; Strecker et al. 1996; Strecker 2006a).

The holotypes and paratypes of the *Cyprinodon* species from Chichankanab were collected and/or described between the years 1949 and 2000. Changes have occurred in the ecosystem that may affect the species. For example, in 1988 the introduction of an *Oreochromis* spp. was registered (Stevenson 1992; Strecker 2006b), in 1996 the invasion of *Astyanax fasciatus* (Strecker 2002), and in 2000, a study registered a nematode infestation with strong prevalence and intensity, which cause an enormous decrease in the relative abundances of the *Cyprinodon* species from Chichankanab (Strecker 2002).

Because no study had included all seven recognized species, changes have occurred in the lake since species description (Stevenson 1992; Strecker 2002, 2006b), species hybridization (Strecker 2006a), and their morphological variation have been described using traditional linear morphometry and anatomical observations (Humphries and Miller 1981; Humphries 1984a, b; Strecker 2002, 2005). In the present study, using a more updated sample of *Cyprinodon* species, collected between 2005 and 2015, we analyze the ecomorphological variation and its potential role in the ongoing diversification of the *Cyprinodon* species from Chichankanab, Quintana Roo, Mexico.

Materials and methods

Specimens. Eight species were considered in this study, the seven endemic *Cyprinodon* species, *C. beltrani*, *C. esconditus*, *C. labiosus*, *C. maya*, *C. simus*, *C. suaviium*, *C. verecundus*, and the sister species of these group *C. artifrons* (Strecker 2006a) [Electronic Supplementary Material (ESM) Fig. S1]. Photographs of the specimens used in this study were obtained from three ichthyological collections, Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Centro de Investigaciones y Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV), Mérida, Yucatán, and

Universidad Autónoma de Yucatán (UADY), Mérida, Yucatán, and were supplemented with images of the holotypes and paratypes originally published.

From ECOSUR, we use photographs already classified into species by morphological and molecular tools, from CINVESTAV, we use photographs already classified into species by morphological and molecular tools, and specimens classified into species by morphological tools on which we take the photographs, and from UADY, we use specimens already classified into species by morphological tools on which we take the photographs (ESM Table S1). In this study, we seek to only use adult specimens, to ensure this and have a range of adult sizes, we use the sizes indicated in the original descriptions of the species and scientific literature, using only specimens close to those sizes or larger, and since Strecker (2006b) indicated that the size of the species may be changing in some species (getting smaller *C. maya*) due to changes in the system, to help us ensure the specimens are adults, we review the eye size which changes from juveniles to adults (juveniles present larger eyes in relation to head size). No live specimens were used in this study.

Supporting ecological data. The standard length of the specimens (from the tip of the snout to the posterior end of the caudal peduncle) used in this study was reviewed by a jitter plot including the size of the holotypes and paratypes, followed by an Analysis of variance (ANOVA) to determine differences between species. By a bibliographic revision of quantitative gut content analyses of the seven species of the complex and *C. artifrons* (Stevenson 1992; Horstkotte and Strecker 2005; Miller et al. 2005), a binary matrix was constructed using nine broad diet categories: detritus, plants, bivalvia, worms, crustaceans, larvae of aquatic insects,

gastropods, zooplankton, and teleost. Indicating presence (1), if it has been indicated in the literature that the species feeds on that item, or absence (0) if that item has not been reported as part of its diet. This matrix was analyzed by a non-metric multidimensional scaling (NMDS) using the Jaccard similarity index which did not treat absences as evidence of similarity between groups (Clarke 1993; Kosman and Leonard 2005).

Morphological data. From the eight species, 138 adult specimens were photographed, between six (*C. verecundus*) and 52 (*C. beltrani*) specimens per species, according to availability (Table 1; ESM Table S1). These 138 specimens include 16 holotypes and paratypes, two per species, 80 specimens classified by both morphological and molecular tools (mitochondrial DNA), and 40 specimens classified only by morphological tools. Four of the eight species considered include a percentage of their specimens classified only by morphology, *C. beltrani* 34 specimens classified only by morphology and 16 specimens by morphology and molecular tools; *C. maya* five specimens classified only by morphological and five by morphology and molecular tools; *C. suavium* 17 specimens classified only by morphological; and *C. verecundus* two specimens classified only by morphological and two by morphology and molecular tools.

To quantify shape variation, a configuration of 16 landmarks and 24 semi-landmarks (Fig. 1) was analyzed by geometric morphometric methods (Rohlf 1999; Zelditch et al. 2004). A landmark is a point fixed on an anatomical structure, while semi-landmarks are points between landmarks, which help us include curves, surfaces, or contours of the organism that do not have an anatomical structure on which to fix a landmark. Landmark and

Table 1 Supporting ecological information of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*

Species	n	Years	IUCN	SL H	SL P	SL (Min.–Max) cm	Diet									
							D	P	B	C	LI	G	Z	T		
<i>Cyprinodon artifrons</i>	15	2005, 2015 *1936	LC	4.14	4.28	2.02 (1.89–4.28)	1									
<i>Cyprinodon beltrani</i>	52	2008, 2009 *1949	VU	3.58	3.11	3.70 (3.17–4.20)	1	1								
<i>Cyprinodon esconditus</i>	7	2009 *1999	VU	3.13	3.02	2.75 (1.96–3.47)	1			1	1					
<i>Cyprinodon labiosus</i>	14	2009 *1974	VU	3.34	3.60	3.16 (2.86–3.35)	1			1	1	1				
<i>Cyprinodon maya</i>	12	2006, 2008, 2009 *1974	VU	6.25	5.63	3.51 (1.81–6.25)	1	1	1	1		1				1
<i>Cyprinodon simus</i>	13	2008 *1974	NT	2.27	2.4	3.03 (2.27–3.73)	1								1	
<i>Cyprinodon suavium</i>	19	2009 *2000	VU	2.98	2.97	3.27 (2.93–3.69)	1		1	1		1				
<i>Cyprinodon verecundus</i>	6	2008, 2009 *1979	VU	2.83	2.72	2.83 (1.44–3.49)	1		1	1	1	1				

n Number of specimens analyzed per species

Years: indicated the year in which the species used in this study were collected and mark with an asterisk the year in which the holotypes and paratypes were collected or described

IUCN red list categories: LC least concern, VU vulnerable, NT near threatened

SL H Standard length of holotype, SL P standard length of paratype

SL: mean standard length of specimens studied

Items in the diet, D detritus, P plants, B bivalvia, C crustaceans, Li larvae of aquatic insects, G gastropods, Z zooplankton, T teleost

semi-landmark configurations were superimposed using a generalized Procrustes analysis (Bookstein 1991; Rohlf 1999) to obtain a matrix of shape coordinates. With the shape matrix of the whole sample, cluster analysis using Euclidean distance was calculated to determine the level of overlap between species, the morphological variation was tested by Principal Component Analysis (PCA) to detect possible groups of species, and lastly, the species were analyzed for statistical differences using permutational multivariate analysis of variance (PERMANOVA), a non-parametric test of differences between two or more groups (Anderson 2021). To get a better appreciation of the relationship of the species, the first four PCs were included in a jitter plot marking the holotypes and paratypes, a simplified PCA using the consensus configuration of the species, and two simplified clusters, one using the holotypes and paratypes morphology, and a second using the consensus configuration of the species were developed. The cophenetic correlation coefficient (CCC) was used as a measure of the goodness of fit of the dendrograms to the original data (Sokal and Rohlf 1962).

Finally, using jitter plots, five body measurements were analyzed, including the holotypes and paratypes of the species: length of the cephalic region, eye, jaw, caudal peduncle height, and maximum body height (Fig. 1). Lengths were standardized using the standard length, by dividing the standard length by each length and expressed as times in the standard length (TSL), i.e., the times the structure fit in the standard length.

Since it has been indicated that no statistical differences were found between some species using mitochondrial DNA, but significant genetic structuring among species was evident (Strecker 2006a), we considered the genetic classification of the species as a hypothesis to prove, running different sets of PCA, all including the holotypes and paratypes. First, using all the data, indicating which specimens were identified by morphology and which by both morphology and molecular tools, a second only including the specimens identified by both morphology and molecular tools, a third including the four species including specimens classified by only morphology and morphology and molecular tools, and a fourth PCA using the consensus morphology of each classification, i.e. only morphology vs. morphology and molecular tools. Finally, to determine if there are statistical differences between classifications, ANOVA was run using the consensus morphology of each classification of the four species including both specimen classifications. Geometric morphometric analyses were performed in the tps software series (Rohlf 2015), and static analyses were completed in PAST V 4.05 (Hammer et al. 2001).

Results

Supporting ecological data. The jitter plot using the size (Fig. 2a) shows that the largest specimens belong to *Cyprinodon maya* (max. 6.25 cm), however, this species shows the second-largest mean value (3.51 cm), and the largest mean belongs to *C. beltrani* (mean 3.70 cm). Two species present the smaller mean sizes *C. esconditus* and *C. verecundus* (2.75 cm; 2.83 cm). While *C. simus*, *C. labiosus*, and *C. suaviium* present average mean values (3.03 cm, 3.16 cm, and 3.27 cm). Finally, *C. artifrons* presents the smallest mean size (2.02 cm). *Cyprinodon artifrons* and *C. maya* are the only two species where the holotypes and paratypes are not in the range of the species analyzed. ANOVA only shows differences between *C. beltrani* as the largest species and the rest of the species *C. artifrons*, *C. esconditus*, *C. labiosus*, *C. simus*, and *C. verecundus* (Table 2).

On the other hand, the NMDS first axis of the diet (Fig. 2b) segregates in the positive edge the species that consume four or more items including bivalvia and gastropoda as *C. maya*, *C. suaviium*, *C. verecundus*, and *C. labiosus*, from the species that consume maximum three items not including bivalvia and gastropoda, *C. beltrani*, *C. simus*, *C. artifrons*, and *C. esconditus*. From the first group with the wider diet, *C. maya* segregates in the positive edge of the second axis due to the presence of teleost and plants in its diet, while teleost is an exclusive item for this species,

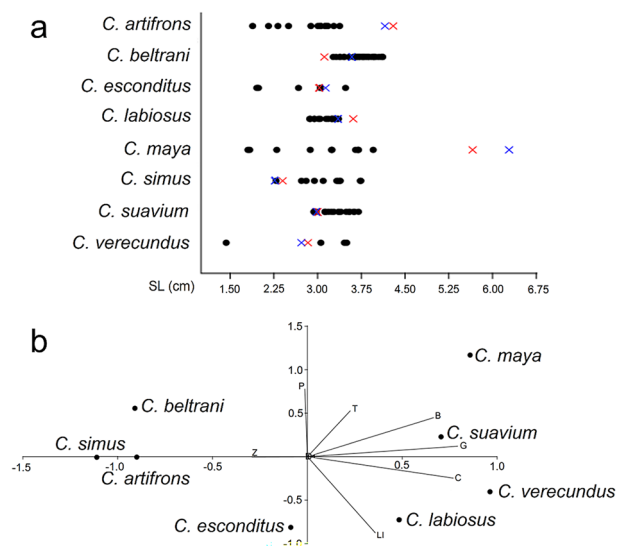


Fig. 2 **a** Jitter plot of the variation in size (SL: standard length, cm) of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*. Holotypes and paratype, red x female, blue x male; black dot specimens used in this study. **b** Non-metric multidimensional scaling (NMDS; stress: 0.1486) on the feeding item on the diet of the species. Items in the diet, D detritus, P plants, B bivalvia, C crustaceans, Li larvae of aquatic insects, G gastropods, Z zooplankton, T teleost

Table 2 Analysis of variance (ANOVA) using the size of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*. *p* values above the diagonal and Tukey's *Q* values below the diagonal. Statistically significant differences indicated in bold

	<i>C. artifrons</i>	<i>C. beltrani</i>	<i>C. esconditus</i>	<i>C. labiosus</i>	<i>C. maya</i>	<i>C. simus</i>	<i>C. suavium</i>	<i>C. verecundus</i>
<i>C. artifrons</i>		0.001	0.9606	0.998	0.291	1.000	0.881	0.996
<i>C. beltrani</i>	5.861		0.0011	0.026	0.976	0.004	0.087	0.009
<i>C. esconditus</i>	1.523	5.995		0.742	0.076	0.961	0.379	1.000
<i>C. labiosus</i>	0.951	4.674	2.281		0.696	0.999	0.999	0.918
<i>C. maya</i>	3.280	1.388	4.137	2.384		0.350	0.929	0.203
<i>C. simus</i>	0.044	5.484	1.523	0.872	3.132		0.914	0.996
<i>C. suavium</i>	1.898	4.061	3.063	0.882	1.704	1.772		0.658
<i>C. verecundus</i>	1.035	5.140	0.354	1.753	3.541	1.047	2.467	

plants are an item shared with *C. beltrani*, which segregates from the group with the restrictive diet. As well, from the first group with the wider diet, *C. labiosus* is located in the negative extreme of the second axis due to the presence of larvae of aquatic insects which share with *C. verecundus* and *C. esconditus*. Finally, crustaceans are an item shared by five of the seven species, *C. esconditus*, *C. labiosus*, *C. maya*, *C. suavium*, and *C. verecundus*, except *C. beltrani* and *C. simus*. All feed on detritus.

Morphologic variation. The cluster analysis of the whole sample shows an intricate pattern with overlap between all the species. The cluster is divided into three main groups, one with *C. artifrons* and *C. beltrani* with the holotypes and paratypes of *C. artifrons*, and one of *C. beltrani*. A second includes specimens of *C. beltrani*, *C. suavium*, *C. maya*, *C. esconditus*, and *C. simus*. The third group includes specimens of all species, and holotypes and paratypes of all species but *C. artifrons*. In this third group, *C. beltrani* is the basal species of two subgroups, one integrated by specimens of *C. esconditus*, *C. suavium*, *C. simus*, *C. labiosus*, *C. maya*, *C. verecundus*, and *C. artifrons*, with the holotypes and paratypes of *C. esconditus*, *C. suavium*, and *C. simus*. The second was integrated by specimens of *C. verecundus*, *C. labiosus*, *C. maya*, and *C. artifrons*, with the holotypes and paratypes of *C. verecundus*, *C. labiosus*, and *C. maya* (Fig. 3a).

When using only the holotypes and paratypes (Fig. 3b), *C. artifrons* first segregate as basal species from the *Cyprinodon* of Chichankanab. From the seven *Cyprinodon*, *C. beltrani* first segregate as basal species of the group, then three groups are formed, *C. maya* and *C. verecundus* form a group; *C. labiosus* and *C. simus* form another group, however, the holotype and paratype of *C. labiosus* separate. The third group is integrated by *C. esconditus* and *C. suavium*.

Finally, using the consensus shapes (Fig. 3c) *C. artifrons* separates first. Then two groups are formed, one including *C. beltrani*, *C. simus*, and *C. suavium*, and a second including *C. labiosus*, *C. esconditus*, *C. verecundus*, and *C. maya*. The patterns conserved in the three clusters were, *C. artifrons*

as the sister species of the group, *C. beltrani* is basal to the group, and the morphological closeness of *C. maya* and *C. verecundus*. PERMANOVA ($F=9.49$; $p=0.0001$) shows differences between most species but *C. esconditus*, *C. verecundus*, and *C. maya* (Table 3).

The PC1 of the analysis using the seven species and *C. artifrons* (Fig. 4a) sum 32% of the variance and mainly segregates in the positive axis *C. artifrons* and *C. labiosus* from *C. beltrani* in the negative axis. In the PC2, which adds 16% to the variation, *C. artifrons* in the negative axis, is segregated from *C. labiosus* in the positive axis. The rest of the species are located in the center of both axes. In the PC1-, *C. beltrani* segregates due to an angular short head, and the lower jaw insertion is posterior to the superior edge of the mouth, producing an $\sim 120^\circ$ angle of insertion, a deep and long trunk, and an elongated and thin caudal peduncle. In the PC1+/PC2+ *C. labiosus* presents the contrary characteristics, a downward deep head profile, the lower jaw is anterior than the superior edge of the mouth, producing an $\sim 70^\circ$ angle of insertion, the trunk is short and slender, and the caudal peduncle is short and deep, while in the PC1+/PC2-, *C. artifrons* shows a short and deep body.

The PCA using only the consensus shapes shows a clearer pattern (Fig. 4b). PC1 sums 44% of the variance and PC2 adds 30%. In the PC1-, closer to the extreme of the axis, there is a cluster of three species *C. suavium*, *C. beltrani*, and *C. simus*, still in the PC1- but closer to the axis intersection is *C. esconditus*. The abdomen of *C. beltrani* is extended and protruded, producing a more angular ventral profile towards the head and a deeper and longer trunk, the position of the dorsal fin is over the anal fin but little anterior than in *C. simus*, *C. suavium*, and *C. esconditus*. On the other extreme of this variation, *C. esconditus* presents a less protruded abdomen and more elongated cephalic profile, elongated body, and the dorsal fin is located posterior than in *C. beltrani*, *C. simus* and *C. suavium*. In *C. beltrani*, the position of the pectoral fin is further down than the mouth and the inferior edge of the interopercle, while in *C. esconditus* the superior edge of the pectoral fin is a little bit higher

Fig. 3 Cluster analyses of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*. Cophenetic correlation coefficient (CCC). **a** Cluster analysis using the complete sample, and the holotypes and paratypes which are indicated with an asterisk. **b** Cluster using only the holotypes and paratypes. **c** Cluster using the consensus shapes per species

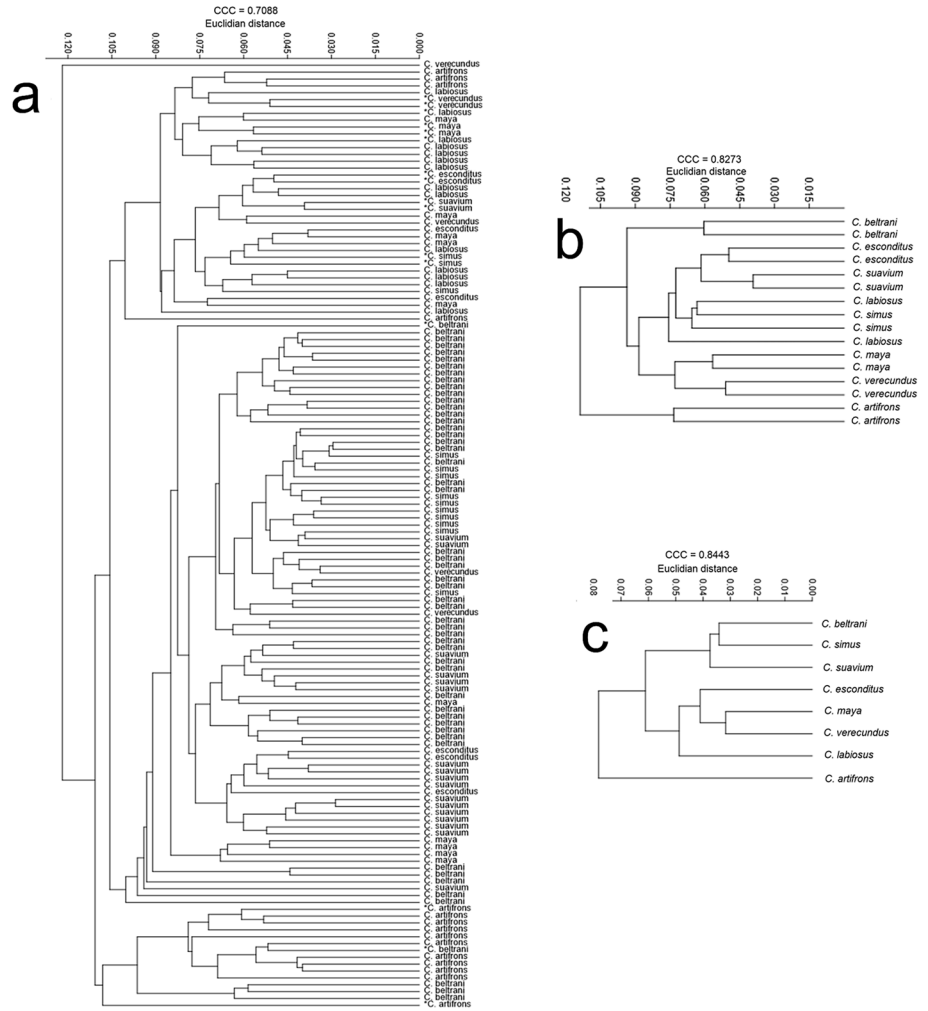


Table 3 Permutational multivariate analysis of variance of the morphological analyses of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*. *p* values above the diagonal and *F* values below the diagonal. Non-statistically significant differences indicated in bold

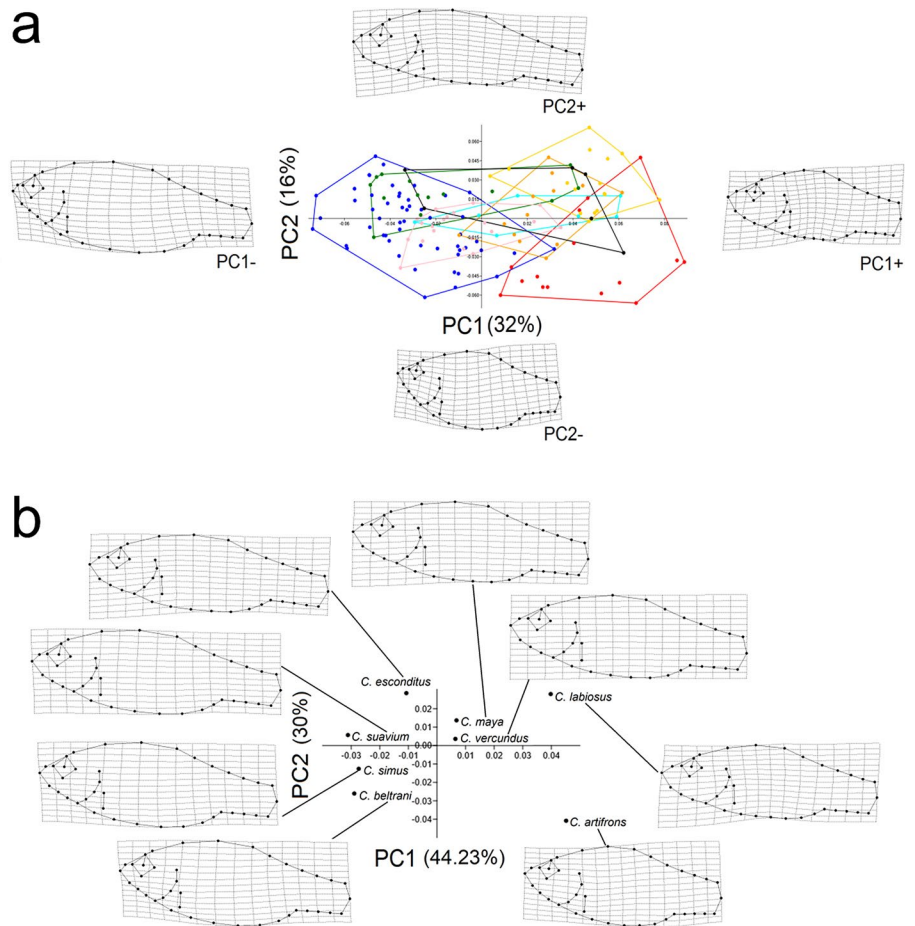
	<i>C. artifrons</i>	<i>C. beltrani</i>	<i>C. esconditus</i>	<i>C. labiosus</i>	<i>C. maya</i>	<i>C. simus</i>	<i>C. suavium</i>	<i>C. verecundus</i>
<i>C. artifrons</i>		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0007
<i>C. beltrani</i>	22.44		0.0001	0.0001	0.0001	0.0005	0.0001	0.0001
<i>C. esconditus</i>	7.658	9.056		0.0049	0.2584	0.0028	0.0054	0.1479
<i>C. labiosus</i>	11.26	26.14	2.883		0.0003	0.0001	0.0001	0.0109
<i>C. maya</i>	7.124	11.07	1.254	4.115		0.0001	0.0003	0.5486
<i>C. simus</i>	14.42	4.431	4.593	10.88	5.686		0.0013	0.004
<i>C. suavium</i>	19.8	6.596	4.162	15.18	5.643	3.771		0.0011
<i>C. verecundus</i>	3.965	8.532	1.568	2.28	0.8739	4.328	4.976	

than the inferior edge of the mouth and the inferior edge of the pectoral fin is align with the inferior edge of the interopercle, as well, the superior and inferior edges of the mouth in *C. esconditus* are aligned (~90° angle), while in *C. beltrani* they are arranged in a ~120° angle. In *C. beltrani* the posterior edge of the dorsal fin is located anterior to half the anal fin, while in *C. esconditus* the posterior edge of the dorsal

fin is posterior to half the anal fin. In this way, *C. simus* and *C. suavium* present intermedium morphological variation between *C. beltrani* and *C. esconditus* (Fig. 4b).

In the PC1+, closer to the axis intersection are *C. maya* and *C. verecundus*, and then closer to the edge of the axis are *C. labiosus* and *C. artifrons*. *Cyprinodon maya* and *C. verecundus* are morphologically similar, *C. maya* presents

Fig. 4 **a** Principal components analyses (PCA) on the variation of the body-shape of *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons* using the complete sample. The transformation grids represent the edge of each axis. Color code: red, *C. artifrons*; blue, *C. beltrani*; aqua, *C. esconditus*; yellow, *C. labiosus*; orange, *C. maya*; green, *C. simus*; pink, *C. suavium*; black, *C. verecundus*. **b** PCA on body-shape variation using the consensus shapes by species. The transformation grids represent the consensus morphology of each species against the mean.



a slenderer body, the superior edge of the pectoral fin is aligned to the inferior edge of the mouth, and the inferior edge of the pectoral fin aligns with the inferior edge of the interopercle, while *C. verecundus* presents a little deeper trunk and the position of the pectoral fin is a little lower than the inferior edge of the mouth and the inferior edge of the interopercle. In both species, the superior and inferior edges of the mouth are aligned ($\sim 90^\circ$ angle), and the posterior edge of the dorsal fin is posterior to half the anal fin.

On the extreme of the PC1+ and PC2+ is *C. labiosus*, which presents opposite characteristics to *C. beltrani*, both species represent extremes *C. beltrani* of PC1 and *C. labiosus* of PC2. *Cyprinodon labiosus* presents a slender body, the head is elongated, the mouth is larger, the trunk is short, and the caudal peduncle is deep. The superior edge of the pectoral fin is a little up than the inferior edge of the mouth and the inferior edge of the pectoral fin aligns with the inferior edge of the interopercle; the inferior and superior edges of the mouth from a $\sim 70^\circ$ angle and the position of the dorsal fin is almost completely over the anal fin. Lastly, *C. artifrons* shows a deep and short trunk and caudal peduncle, the superior and inferior edges of the mouth are aligned, the position of the pectoral fin is further down than the mouth and the

inferior edge of the interopercle, and the posterior edge of the dorsal fin is posterior to half the anal fin (Fig. 4b).

The jitter plots of the first four principal components of the geometric morphometric data showed the holotypes and paratypes in the range of the specimens used (Fig. 5). In the plot of the first and second PCs, the holotype and paratype of *C. maya* looks a little out of phase, however, in PC3 and PC4 it looks among the range. As can be observed in these plots *C. artifrons*, *C. beltrani*, and *C. labiosus* are the species that segregate more from the group.

The jitter plots of the body measurements showed the holotypes and paratypes generally in the range of the specimens used (Fig. 5). Only *C. maya* looks a little out of phase in the jaw measurement. As in the geometric morphometric analyses, *C. artifrons*, and *C. beltrani* are the ones that segregate more from the group. The cephalic measurements show *C. artifrons* and *C. labiosus* as the species with the largest cephalic region in TSL, *C. beltrani* shows a wide range, and the rest of the species show similar mean range. The species with the largest eyes are *C. artifrons*, *C. simus*, and *C. verecundus*, again *C. beltrani* presents a wide variation, *C. maya* and *C. labiosus* show the smallest eyes, and *C. esconditus* and *C. suavium* mean sizes. The larger jaws

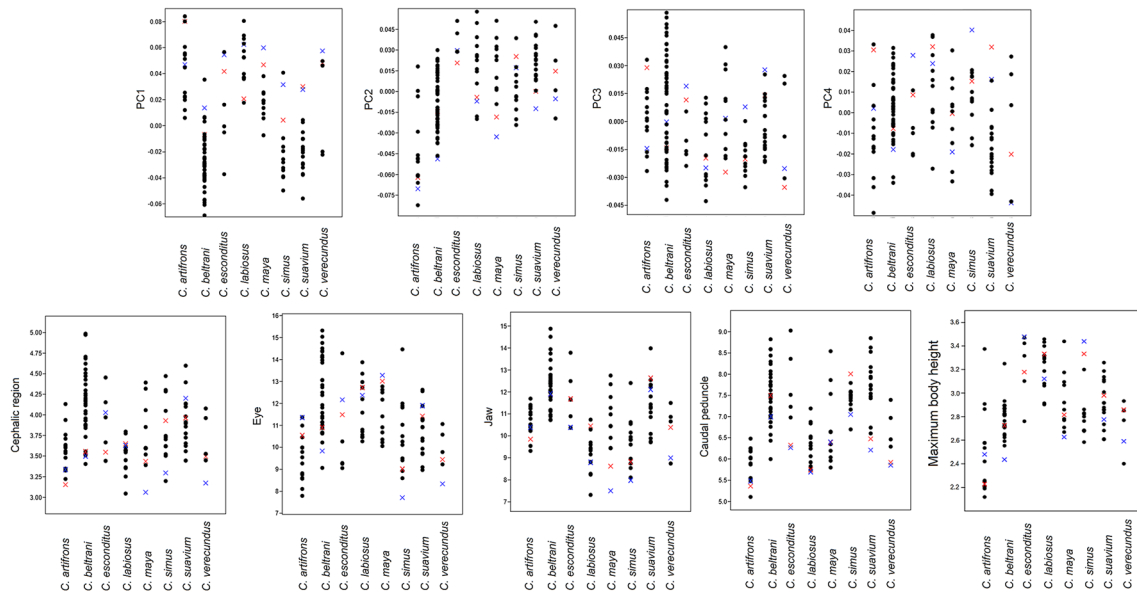


Fig. 5 Jitter plots of the *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*. x Holotypes and paratypes; red x female, blue x male; black dot specimens used in this study. Above: scores of

the first four principal components (PC) of the geometric morphometric analyses. Bottom: standardized body measurements as times in the standard length (TSL)

belong to *C. labiosus*, *C. maya*, and *C. simus*, the smallest to *C. beltrani*, *C. esconditus*, and *C. suaviium*, while *C. verecundus* and *C. artifrons* presented mean sizes. The species with the highest caudal peduncle is *C. artifrons*, followed by *C. verecundus* and *C. labiosus*, the rest of the species present mean highs. Finally, *C. artifrons* presents some of the higher body specimens, however, it presents a wide variation including covering most of the variation of the seven species, among the Chichankanab species, *C. beltrani* and *C. verecundus* presents the highest bodies, the rest of the species present mean values (Fig. 5).

Finally, using the geometric morphometric data, four PCA comparing classification tools, morphological vs. morphological and molecular tools were carried out, showing similar patterns and no statistical differences between classifications. ANOVA results between *C. beltrani* $F=0.2866$; $p=0.5932$; *C. maya* $F=0.9032$; $p=0.3434$; *C. suaviium* $F=0.9808$; $p=0.3766$; *C. verecundus* $F=0.9258$; $p=0.3375$.

The pattern between the whole sample (Fig. 6a) and just those classified by both morphological and molecular tools (Fig. 6b) is similar since most specimens were classified by both tools. The PCA of the species that include both classifications (Fig. 6c) shows an overlap between classifications for *C. maya* and *C. beltrani*. In the PCA using the consensus shapes (Fig. 6d), we can observe that the consensus of *C. maya* and *C. beltrani* classified by morphology are closer to those classified by both morphological and molecular tools than to the holotypes and paratypes, while in *C. verecundus* the consensus classified only by morphological data are

closer to the holotype and paratype than to the specimens classified by both morphological and molecular data, finally, the sample of *C. suaviium* includes holotype and paratype, and specimens classified only by morphological tools, however, ANOVA did not show differences between them.

Discussion

An important topic to first discuss is the possibility of wrong determination due to the difficulty in distinguishing the nominal species, especially knowing there is hybridization ongoing (Strecker 2006a) and changes occurring in the ecosystem (Fuselier 2001; Strecker 2006b) since the species were first described. To ensure we used the correct specimens, we included the holotypes and paratypes of the species in the morphological comparison, more than half of our sample was diagnosed by both morphological and molecular tools, and, statistical analyses were done to ensure that the sample only diagnosed by morphological characters was not significantly different than that diagnosed by both morphological and molecular variables.

The cluster plot using the whole sample (Fig. 3) does not show a completely cohesive pattern among species. It is divided into three main groups; the basal cluster segregates *Cyprinodon artifrons* and *C. beltrani* with their holotypes and paratypes. Corroborating the differential morphology of these species, since *C. artifrons* is the sister species of the group and *C. beltrani* is the basal species of the *Cyprinodon* from the Chichankanab (Humphries and Miller 1981;

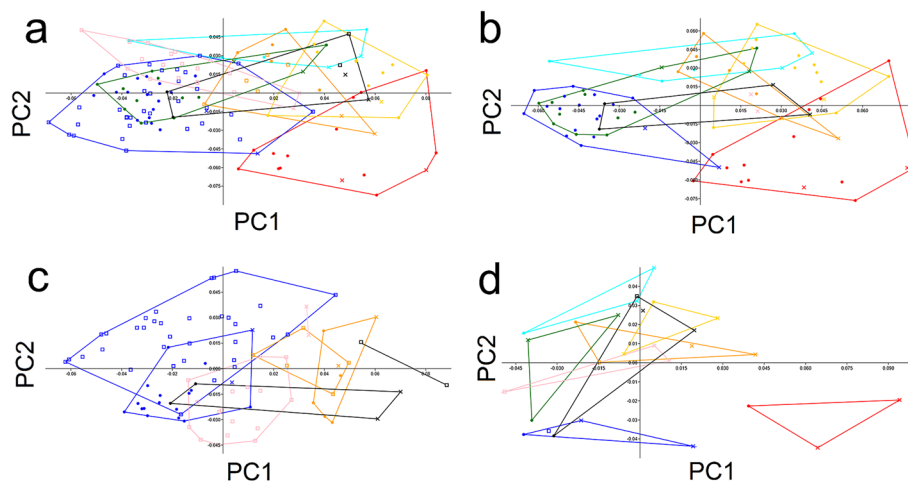


Fig. 6 Principal components analyses (PCA) on the variation of the body-shape of *Cyprinodon* species from the Chichankanab lagoon and *C. artifrons*, using **a** the complete sample, **b** only the specimens identified by both morphological and molecular tools, **c** only the species that include specimens identified by only morphology and by both morphological and molecular tools, and **d** mean shape of the specimens identified by only morphology and by both morpho-

logical and molecular tools. *Cross* Holotypes and paratypes, *squares* specimens identified by morphological tools, *dots* specimens identified by both morphological and molecular tools. Color code: *red*, *C. artifrons*; *blue*, *C. beltrani*; *aqua*, *C. esconditus*; *yellow*, *C. labiosus*; *orange*, *C. maya*; *green*, *C. simus*; *pink*, *C. suavium*; *black*, *C. verecundus*

Horstkotte and Strecker 2005). Most holotypes and paratypes are in one cluster, although, they are not grouped by species, this group may represent the morphology of the species when collected for the original descriptions (1949–2000) and some specimens with strong similarity to those morphologies. A second cluster, which does not include holotypes and paratypes, shows more consistency among species, which may indicate the state of the morphology in the range of time of the sample (2005–2015).

Based on our analysis of variance, using the geometric morphometric results, most species are distinguishable from each other, but three species, *C. esconditus*, *C. verecundus*, and *C. maya*. A supporting variable that can help in the segregation of *C. maya* is the size; *C. maya* showed a mean SL (standard length) of 3.51 cm, while *C. esconditus* 2.75 cm and *C. verecundus* 2.83 cm, and the body measurements can help us segregate *C. esconditus* which presents a shorter cephalic region, eye, and jaw in TSL, than *C. verecundus*. Thus, with these specimens and these variables, we can achieve species segregation using different variables.

Our sample of *C. maya* did not reach the large SL originally described for this species (male SL = 6.25 cm; female SL = 5.63 cm; Humphries and Miller 1981). In this regard, Fuselier (2001) indicated that the presence of *Oreochromis* spp. caused a shift in the use of the habitat of *C. maya* and *C. labiosus* pushing them to habitats occupied by *C. beltrani*. Later, Strecker (2006b) indicates that the large sizes of *C. maya* documented before the cichlid invasion were not detected in all the subsequent sampling, where no *C. maya* specimens were observed with a standard length surpassing

5 cm. The mean standard length of the *C. maya* specimens used in our analyses was 3.51 cm, and they were collected between the years 2006, 2008, 2009, and 2011. Size depends on the intrinsic characteristics of the species and environmental variables. The environmental stressors may cause slower growth and alter the age and size of maturity, forcing the maximization of fitness by changing the life history tactics to mature earlier at smaller sizes (Berrigan and Koella 1994). Thus, the smaller sizes may be a response to the changes and pressures imposed by the environment.

In Fig. 4, we can notice the holotype and paratype of *C. maya* show larger jaws than the rest of the *C. maya* sample. Yet, in the other body measurements, the difference between the holotype, paratype, and the rest of the sample is not as strong as in the jaw. To determine if the characteristic large jaw of *C. maya* is changing or if our findings are the result of the use of hybrid (Strecker 2006a) or younger specimens, actualized sampling and morphological analyses supported by molecular analyses are needed, thus we recommend discretion when analyzing our results of *C. maya*.

The morphological variation found in this study indicates some lines of morphological diversification between the *Cyprinodon* species of Chichankanab in the cephalic profile, trunk, caudal peduncle, fins, mouth, and eyes. Trunk morphology is related to stability and thrust (Drucker and Lauder 2001, 2005; Fulton 2007; Standen 2008). In this way, deep trunks favor stability at slow swimming speeds and are likely advantageous in structurally complex habitats (Aguilar-Medrano et al. 2016). While long, slender trunks favor fast swimming, which is advantageous for exploiting

midwater and near-surface habitats (Webb and Weihs 1986; Lauder 2000). Thus, we can hypothesize that the use of the ecosystem was an important character that allows the diversification of this group, favoring stability in *C. beltrani*, *C. simus*, and *C. suavium*, and speed in *C. labiosus*, *C. esconditus*, *C. verecundus*, and *C. maya*.

Cyprinodon beltrani has the deepest trunk, a mouth with an insertion angle of $\sim 120^\circ$, the largest size (μ SL 3.70 cm), as well as the largest intestine, about six to eight times its SL, is more abundant on soft substrates (sand and gravel) around the lake margin, in loose aggregations, feeding on detritus and plant matter from the bottom (Humphries and Miller 1981; Horstkotte and Strecker 2005; Horstkotte and Plath 2008). Because algae and detritus are poor in nutrients (Wilson et al. 2003), herbivores and detritivores have long digestive tracts to extract adequate nutrition from these resources (Elliott and Bellwood 2003). Therefore, the deep trunk may be related to a long intestine in *C. beltrani*.

Cyprinodon suavium also has a deep trunk, which is not only related to a protruding abdomen but also a small hump, it is one of the largest species of the group (μ SL 3.27 cm), it has a relatively long caudal peduncle, it feeds of benthic mollusks, such as snails, ostracods, and bivalves (Strecker 2005). A hump increases drag (Portz and Tyus 2004), in other species it has been related to sexual selection (Bonduriansky and Rowe 2005), it has been suggested to be an advantage to defend against predation by increasing body depth (Portz and Tyus 2004), and it can also help to support stronger muscles to exert powerful compressive forces to feed on hard-shelled animals.

Cyprinodon simus has a short intestine (Horstkotte and Strecker 2005) and according to Humphries and Miller (1981), it feeds on zooplankton, however, it has a deep trunk, and according to a more updated analysis (Horstkotte and Strecker 2005), detritus represents 99% relative importance in its diet. It also has a vertical lower jaw and therefore the opening of the mouth is superior. According to Elias-Gutierrez et al. (2001) and Horstkotte and Strecker (2005), the lake now has almost no zooplankton, which is indicated as the reason for the decline in the *C. simus* population. In this way, the availability of food is a strong force in the divergence of this group, where changes in the availability of a resource produce disadvantageous scenarios for the species specialized in its consumption, producing a decrease in the population, a new adaptation process to other resources, or the extinction of the species.

Although *C. beltrani*, *C. simus*, and *C. suavium* have similar morphologies, they differ in some characteristics that allow them to access a different diet. Furthermore, these three species differ in size, *C. beltrani*, and *C. suavium* are two of the three largest species of the group (with *C. maya*), while *C. simus* is the third smallest species. Size influences the competitive ability, resource utilization, and ecological

niche of a species (Malerba et al. 2017), also many life-history traits covary with body size (Peters 1983; Reznick et al. 1990), for example, smaller species tend to grow faster (Savage et al. 2004) and have a shorter lifespan (Marba et al. 2007; Malerba et al. 2017). In this way, although the morphology is similar, the size allows niche differentiation in these species.

On the other hand, *C. labiosus*, *C. esconditus*, *C. verecundus*, and *C. maya* are carnivorous species (Horstkotte and Strecker 2005), and have elongated bodies and vary in the depth of the caudal peduncle. An elongated trunk reduces drag when swimming favoring speed, but both the trunk and the caudal peduncle work together to increase and maintain speed during locomotion (Fulton 2007; Aguilar-Medrano et al. 2016). *Cyprinodon esconditus* has a slenderer and more elongated peduncle than the rest species of the clade, which favors swimming speed and efficiency (Videler 1993; Fulton 2007; Aguilar-Medrano et al. 2013), while *C. labiosus* and *C. verecundus* have a deeper caudal peduncle, which facilitates strong initial swimming bursts (Fulton 2007). In this way, *C. esconditus* could be a more efficient long-distance swimmer, while *C. labiosus* and *C. verecundus* can use this strong burst to hunt, push, or escape from predators.

Following this idea, *C. labiosus* is a carnivorous species that presents fleshy lips, with a larger lower lip. The long snout of *C. labiosus* has been indicated to be suitable for searching for invertebrates among pebbles (Horstkotte and Plath 2008), this being the case, a fleshy, strong, and long lower lip would be useful, as well as a deep caudal peduncle that facilitates a strong swimming burst, which can also be useful for pushing pebbles.

Cyprinodon maya shows a mean morphological variation between *C. esconditus*, *C. labiosus*, and *C. verecundus*, that is, an elongated body, with a deep caudal peduncle; it also differs from these species by presenting one of the largest sizes of the group (μ SL 3.51 cm). In addition, *C. maya* has the broadest diet and is the only species in the group that feeds on fish. In this way, we can consider *C. maya* as a predator, with highly energetic consumption, which is related to both diet and size (Tang et al. 2017).

Different studies have found that the trunk, the dorsal, pelvic, and anal fins make a module associated with stability and thrust, and specifically the pectoral fin with maneuverability (Drucker and Lauder 2001, 2005; Fulton 2007; Standen 2008). The dorsal and anal fins increase stability by increasing the lateral surface of the body during swimming, but at the expense of increasing drag (Grillner 2011), therefore a small misalignment between them can decrease resistance, especially useful for those species with an already deep trunk. These patterns were corroborated by this study, indicating a relationship between the dorsal, anal, and pectoral fins in this group. In *C. beltrani*, *C. simus*, and *C. suavium* the dorsal and anal fins are less aligned, that is,

the dorsal fin covers less of the anal fin, and the pectoral fin is in a lower position to the mouth, the opposite is observed in *C. labiosus*, *C. esconditus*, *C. verecundus*, and *C. maya*, the dorsal and anal fins are more aligned, and the pectoral fin is more aligned with the mouth.

According to the characters analyzed here, *C. beltrani* is the most divergent species of the group, being specifically segregated by size, morphology, and diet, followed by *C. simus* segregated by morphology and diet, *C. suavium* by size and morphology, *C. maya* by size and diet, and *C. labiosus* by morphology. *Cyprinodon esconditus* and *C. verecundus* are similar in size and morphology, both are carnivores, but *C. verecundus* shows a tendency to molluscivory, a diet shared with *C. suavium*, which presents different size and morphology, on the other hand, the diet of *C. esconditus* is similar to that of *C. labiosus*, which has a different morphology.

In 2004, the Chichankanab Lake was designated a RAMSAR site (No. 1364) justifying its designation by the presence of the endemic *Cyprinodon* group, the presence of early Holocene sediments with remains of *Ammonia beccarii*, and the presence of *Rhizophora mangle* (<https://rsis Ramsar.org/es/ris/1364>). Chichankanab Lake is located on communal land, so to undertake conservation actions in the area it is of utmost importance to collaborate with local representatives of the communal system so that the conservation of the area is made by users and connoisseurs of the resource, who have developed an economic and social identity related to the lake.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10228-024-00980-2>.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval The handling of the specimens was carried out according to the guidelines of each fish collection and the University or Research Center that contains them. All specimens used were preserved specimens as no live specimens were used in this study.

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