

Article



A new species of *Cnesterodon* (Cyprinodontiformes: Poeciliidae) from a small tributary of arroyo Cuñá-Pirú, río Paraná basin, Misiones, Argentina

GASTÓN AGUILER¹, JUAN MARCOS MIRAND¹ & MARÍA DE LAS MERCEDES AZPELICUET²

¹CONICET-Fundación Miguel Lillo, Miguel Lillo 251, CP 4000- San Miguel de Tucumán, Tucumán, Argentina. E-mail: gastonaguilera@csnat.unt.edu.ar; mcmirande@gmail.com

² CONICET-División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Paseo del Bosque 1900, La Plata, Argentina. E-mail: azpeli@museo.fcnym.unlp.edu.ar

Abstract

Cnesterodon pirai new species is described from a small stream, tributary of the arroyo Cuñá-Pirú, río Paraná basin in Argentina. The new species is diagnosed by the following combination of characters: 6 to 8 irregular dashes, ranging from oval to vertical stripes on females and 7 to 9 irregular dashes ranging from oval to circular dots on males; lack of a distal membranous filament on the terminal appendix of ray 3 of the gonopodium; absence of longitudinal dark-brown band along flank; snout long (16.7–28.7 % HL) and pointed; absence of a large post-gonopodium blotch on ventral profile in adult males; absence of dashes along predorsal portion of first, second and third lateral series of scales, associated to the vertical bars on body side; 12–13 epipleural ribs; medial surface of ascending process of premaxilla approximately straight; presence of teeth on fourth ceratobranchial; distal portion of third and fourth gonactinosts separate, except by tip of third gonactinost; fifth gonactinost free; and presence of a constriction on unpaired appendix of gonopodium. In a phylogenetic analysis the new species forms a tricotomy with (*Cnesterodon brevirostratus* + *C. septentrionalis*) and (*C. hypselurus* + *C. iguape*).

Key words: Northeastern Argentina, Salto Encantado, Cnesterodon pirai n. sp., phylogenetic relationships

Resumen

Una nueva especie, *Cnesterodon pirai*, se describe de un pequeño arroyo tributario del arroyo Cuñá-Pirú, cuenca del río Paraná en Argentina. Esta nueva especie se diagnostica por la siguiente combinación de caracteres: 6 a 8 manchas, que van desde formas ovales a barras verticales en las hembras, y de 7 a 9 manchas irregulares que van desde formas ovales a puntos en los machos; ausencia de un filamento distal membranoso en el apéndice terminal del radio 3 del gonopodio; ausencia de una banda marrón oscura en los flancos; hocico largo (16.7–28.7% HL) y puntiagudo; ausencia de una gran mancha post-gonopodio en el perfil ventral de machos adultos; ausencia de manchas, en la porción predorsal de la primera, segunda y tercera serie de escamas, asociadas a las barras verticales en los lados del cuerpo; 12–13 costillas epipleurales; superficie medial del proceso ascendente del premaxilar recto; presencia de dientes en el cuarto ceratobranquial; porción distal del cuarto y quinto gonactinosteo separada, excepto por la punta del tercer gonactinósteo; quinto gonactinosteo libre; y la presencia de una constricción en el apéndice impar del gonopodio. En un análisis filogenético la nueva especie forma una tricotomía con (*Cnesterodon brevirostratus + C. septentrionalis*) y (*C. hypselurus + C. iguape*).

Palabras clave: Nordeste Argentino, Salto Encantado, Cnesterodon pirai n. sp., relaciones filogenéticas de Cnesterodon

Introduction

The genus *Cnesterodon* Garman includes small cyprinodontiform fishes distributed in South America in the río Uruguay and upper río Araguaia basins, the Paraná-Paraguay system and along coastal drainages from São Paulo to Argentina; it is also distributed in small drainages of western Argentina (Lucinda, 2005).

The genus is diagnosed by the possession of the following uniquely derived and unreversed characters: (1) anterior tip of basipterygium sinuous in adult males; (2) outer surface of basipterygium base narrow in adult males; (3) haemal arch and spine of vertebrae 13–17 in adult males modified in rudimentary gonapophyses; (4) gonapophysis of vertebra 14 rudimentary in adult males; (5) distal portion of pleural ribs 6, 7, and 8 in adult males expanded; (6) large basal process on first anal-fin proximal radial in adult males; (7) unpaired appendix at tip of R3; (8) distal segment at tip of R5a transformed in retrorse triangular spine; (9) dark spot posterior to anal-fin base of males continuous ventrally side by side and continuous with ventral median line of caudal peduncle (Lucinda, 2005).

Jenyns (1842) described *Poecilia decemmaculata* Jenyns, which was subsequently considered by Garman (1895) as type species of the genus *Cnesterodon*. A few years later *C. carnegiei* Haseman was described. Almost 82 years occurred between Haseman's (1911) description and the publication of two new species of the genus, *Cnesterodon brevirostratus* Rosa & Costa and *C. septentrionalis* Rosa & Costa, both included in the systematic revision of the genus by Rosa & Costa (1993).

The number of known species increased with the description of *C. omorgmatos* Lucinda & Garavello, *C. hypselurus* Lucinda & Garavello, and *C. raddai* Meyer & Etzel. Lucinda (2003) recognized seven species in this genus. Lucinda & Reis (2005) analyzed the phylogenetic relationships of the subfamily Poeciliinae, confirming the monophyly of *Cnesterodon* and providing a hypothesis of relationships within this genus. Lucinda (2005) reviewed the systematics of the genus, described *C. iguape* Lucinda, and recognized nine valid species including *C.* sp. *B*, a new species under description. More recently, *C. holopteros* Lucinda, Litz & Recuero was described from Uruguay.

Among the nine described species of *Cnesterodon*, only *C. raddai* has its type locality in Argentina. The objective of this paper is to describe a new species of *Cnesterodon* from Argentina which seems endemic from the type locality and to provide a new phylogenetic hypothesis for the genus.

Material and methods

Material examined is deposited in the following collections: Fundación Miguel Lillo (CI-FML), Tucumán, Argentina; Asociación Ictiológica (AI), La Plata, Argentina; Academy of Natural Sciences of Philadelphia (ANSP), Philadelphia, United States of America. Specimens were cleared and counterstained (C&S) following Taylor & Van Dyke (1985). Nomenclature of the cephalic pores follows Rosen & Mendelson (1960), Gosline (1949) and Parenti (1981). Counts taken under stereomicroscope follow Lucinda (2005). In the description, number in brackets following the counts indicates the number of specimens for each count. An asterisk indicates holotype counts. Morphometric data were obtained from digitalized images of the specimens. Thirteen homologous landmarks per specimen were placed at: premaxilary tip; anterior and posterior margins of orbit; postero-dorsal corner of opercle; supraoccipital tip; base of first pelvic-fin ray; origin and end of dorsal-fin base; origin and end of anal-fin base; dorsal and ventral profile of caudal peduncle at minimum peduncle depth; and at base of middle caudal-fin rays. Measurements are straight distances between two landmarks, calculated with the software Image Tool, version 3.00 (Wilcox et al. 2002). From these landmarks the following measures were taken: a—standard length (SL); b—head length (HL); c—snout to occipital distance; d—predorsal distance; e—dorsal-fin base; f— anal-fin base; g—prepelvic length; h preanal length; i—postanal length; j—caudal peduncle depth; k—snout length; l—orbital diameter; and mpost-orbital length. Body depth was measured at maximum depth. Measurements are expressed as percents of SL, excepting the snout and post-orbital lengths and the orbital diameter, which are expressed as percents of HL.

The new species is herein included in the phylogenetic framework proposed by Lucinda & Reis (2005) for the subfamily Poeciliinae. Codification of the new species is shown under "Phylogenetic Relationships" section. Numbers in brackets represent polymorphic states for the character under consideration. A cladistic parsimony analysis was performed with TNT (Goloboff *et al.*, 2003a). All the transformation series were considered as unordered. The analysis was made under both equal and implied weighting (Goloboff, 1993). For details of the analysis under implied weighting see Aguilera & Mirande (2005). Only the phylogeny of the species of *Cnesterodon* is depicted since the obtained relationships of the family on both analyses remain stable from Lucinda & Reis (2005). For both analyses, nodal support was calculated with symmetric resampling (1000 replicates, with 5 addition sequences, saving up to 2 trees each) expressed as values of GC (groups present/contradicted), with a change probability of 0.33 (Goloboff *et al.*, 2003b) and relative Bremer support (Goloboff & Farris, 2001), saving 50000 suboptimal trees.

Comparative material examined (SL in mm): *Cnesterodon decemmaculatus* CI-FML 1749, 104 (30), 15.5–25.7 mm, Argentina, Santa Fe, 9 de Julio, Ruta Nacional 98, entre Vera y Tostado; CI-FML 1783, 23 (10), 23.6–29.2 mm, Argentina, Córdoba, río Villa del Totoral. CI-FML 1772, 65 (20), 13.3–20.4 mm, Argentina, Santiago del Estero, Añatuya, ruta Provincial 21. CI-FML 1624, 94 (20), 14.3–17.7 mm, Argentina, Corrientes, Gral. Paz, Caa-Catí; *Cnesterodon* cf. *decemmaculatus* CI-FML 1668, 36 (20), 19–29.5 mm, Argentina, Tucumán, Dpto. Chicligasta, Ruta Provincial 380, río Gastona; *Cnesterodon holopteros*, AI 242, 6 ex., 12.2–19.2 mm, lagoon near Franquia, Artigas, Uruguay, 30° 13.05' S 57° 37.29' W; Coll. T. Litz, M. Litz, J. Litz, P. Laurino and J. Salvia, March 2003.

Cnesterodon pirai, n. sp. (Fig. 1, 2)

Holotype: CI-FML 3853 male, 26.6 mm SL, Argentina, Misiones, Aristóbulo del Valle, río Paraná basin, arroyo Almeida, tributary of arroyo Cuña Pirú (27° 00' 24" S 54° 50' 22" W). G. Aguilera and J. M. Mirande, December 6, 2004.

Paratypes: CI-FML 3854, 4 ex., 15.5–18.8 mm, collected with holotype; AI 223, 6 ex., 21.0–27.8 mm, Argentina, Misiones, Aristóbulo del Valle, río Paraná basin, arroyo Almeida, affluent of arroyo Cuña Pirú, G. Aguilera, J. M. Mirande and G. Terán, November 23, 2008; ANSP 187060, 4 ex., 21.6–22.8 mm, Argentina, Misiones, Aristóbulo del Valle, río Paraná basin, arroyo Almeida, tributary of arroyo Cuña Pirú, G. Aguilera, J. M. Mirande and G. Terán, November 23, 2008; CI-FML 3855, 2 ex. C&S, 15.9–20.7 mm SL, collected with the holotype; CI-FML 3965, 8 ex., 20.0–28.2 mm, Argentina, Misiones, Aristóbulo del Valle, río Paraná basin, arroyo Almeida, tributary of arroyo Cuña Pirú, G. Aguilera, J. M. Mirande and G. Teran, November 23, 2008.

Diagnosis: Cnesterodon pirai is diagnosed by the combination of the following characters: 6 to 8 irregular dashes on flanks, ranging from oval to vertical stripes on females and 7 to 9 irregular dashes ranging from oval to circular dots on males (dashes both on males and females covering 1 or 2 scales in transverse row); absence of a large post-gonopodium blotch on ventral profile in adult males; lack of a distal filament on gonopodium; absence of longitudinal dark-brown band along flank; snout pointed and long (16.7–28.7 % HL); possession of 12–13 epipleural ribs; medial surface of ascending process of premaxilla approximately straight; presence of teeth on fourth ceratobranchial; distal portion of third and fourth gonactinosts separate, except by tip of third gonactinost; fifth gonactinost free; and presence of a constriction on unpaired appendix of gonopodium.

Description: Body compressed, pre-anal region width about 1.14 of body depth; post-anal region compressed towards peduncle. Dorsal profile slightly concave from snout tip to vertical through middle eye; convex from vertical through middle eye to third or fourth scale anterior to dorsal-fin origin, and straight to dorsal-fin origin; convex from dorsal-fin origin to caudal fin. Preanal profile convex. Anal-fin base oblique dorsally. Postanal profile slightly convex. Dorsal-fin origin at vertical through third anal-fin ray in females

and posterior to anal-fin base in males. Pectoral-fin insertion just ventral to horizontal line through middle of eye. Pelvic fin small, below pectoral-fin insertion in males, and at vertical through end of the longest pectoral-fin ray in females. Anal-fin insertion just anterior to vertical through dorsal-fin origin in females. Gonopodial insertion at vertical through tip of longest pectoral-fin ray in males. Mouth superior.



FIGURE 1. *Cnesterodon pirai* **n. sp.**, CI-FML 3853, holotype, male, 26.6 mm SL (top); CI-FML 3965, paratype, female, 28.2 mm SL (bottom).

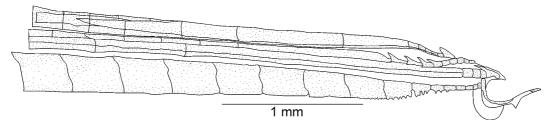


FIGURE 2. Gonopodium of *Cnesterodon pirai*, paratype CI-FML 3855.

Morphometric measurements expressed as percents of SL are presented in Table 1. Counts of 23 specimens including the holotype are as follow: predorsal scales 13 (18*), 14 (4), 15 (1); longitudinal scales series 29 (1), 30 (13*), 31 (8), 32 (1); transverse scales 10 (22*), 11(1); scales around the peduncle 16 (23*); dorsal-fin rays 8 (23*); anal-fin rays (females) 10 (15); pectoral-fin rays 11 (1), 12 (22*); caudal-fin rays 25 (1), 26 (16*), 27 (6). Counts on C&S specimens are as follow: pelvic-fin rays: 4(2) (males), 5(1) 6(1) (females); pleural ribs 14(3), 15(1); epipleural ribs 12 (3), 13 (1); vertebrae 31 (1), 32 (3); gonopodial rays (males) 8 (2).

TABLE 1. Descriptive morphometrics of specimens of *Cnesterodon pirai*.

Morphometric measures	holotype	males (n=8)		females (n=15)	
Character		mean	range	mean	range
Standard length (mm)	26.6	22.5	19.8–26.6	24.0	21.8–27.8
Percent of standard length					
Head length	19.5	21.1	19.3–22.6	22.9	20.8–26.3
Snout-occipital	19.3	20.3	18.9–22.7	20.7	18.7–23.9
Predorsal distance	52.4	52.8	50.5- 54.5	60.7	57.5-62.9
Dorsal-fin base length	10.8	11.0	9.6–12.2	11.0	9.1–14.5
Anal-fin base length	6.9	7.3	6.6–8.3	9.2	7.7–10.4
Body depth	21.1	20.0	19.2–21.2	25.9	22.6–29.8
Pre-pelvic length	23.4	24.9	23.2–27.2	44.1	41.7–46.4
Pre-anal length	33.2	33.0	30.8-35.1	57.3	54.4–59.3
Post-anal length	64.6	65.2	61.7–70.1	36.4	34.5–39.2
Caudal peduncle depth	16.1	16.0	14.9–17.4	14.4	13.7–15.6
Percent of head length					
Snout length	19.7	20.9	16.7–25.9	22.2	16.8–28.7
Orbital diameter	36.1	37.4	34.6–40.2	37.5	30.6–42.8
Postorbital length	46.3	47.3	41.1–53.2	55.1	49.6–60.6

Gonopodium (Fig. 2): Gonopodial complex composed of 9 gonactinosts. Gonactinosts 2, 3, and 4 fused. Eight anal-fin rays. R1 unbranched with 7 segments. R2 unbranched with 8 segments. R3 with 25 segments, tiny serrations at subdistal segments, and a bony style at tip. Bony style not completely ossified, slender, curved dorsally, with a ventral chondral apophysis. Semicircular membrane reaching middle of bony style, not forming a distal filament. Posterior ramus of R4 with four pairs of retrorse spines located on segments 7 to 10 before tip. Distal portion of R5 curved dorsally, ending in a retrorse claw. R6 and R7 branched and distal segments partially ankylosed.

Cephalic sensory system: Preorbital ramus composed by 4 superficial neuromasts. Anterior portion of supraorbital ramus (pores 1 and 2a) composed by 3 neuromasts; posterior portion of supraorbital ramus (pores 2b, 3 and 4) composed by 3 neuromasts. Infraorbital ramus composed by 3 superficial neuromasts (pores 4b, 5 and 6a), and a groove with 1 neuromast (pores 6b and 7). Preopercular ramus composed by a vertical groove with 3 neuromasts, and an inferior canal with 4 pores. Mandibular ramus composed by 5 superficial neuromasts.

Coloration of live specimens: Body dorsum yellowish green, darker from midlateral region to ventral portion of body; belly white; iridescent green blotch on opercle; fins light yellow.

Coloration of preserved material: Background yellowish; reticular pattern formed by dark brown chromatophores following border of scales. Predorsal line very faint or absent. Dashes on flanks formed by dark-brown chromatophores covering 1 or 2 scales (never reaching dorsal and ventral profile of body), mostly on midline; females with 6 to 8 irregular dashes, ranging from oval to vertical stripes, and males with 7 to 9 irregular dashes ranging from oval to circular dots. Males with or without blotch of dark-brown chromatophores on flanks situated opposite to dorsal-fin insertion, below midline of body side; blotches wider dorsally and narrowing to ventral portion, contacting or not each other ventrally. Midventral postanal line contacting or not ventral portion of blotches, and extending to caudal fin.

Distribution: Cnesterodon pirai is only know from its type locality, arroyo Almeida, affluent of arroyo Cuñá-Pirú, río Paraná basin, Aristóbulo del Valle, Misiones, Argentina (Fig. 3). In spite of the collecting effort

in different streams of Misiones province, especially in the Cuñá-Pirú basin, *C. pirai* was not found in other sites.

Ecological notes: The stream where the new species lives is narrow (2 m wide on its widest section) and shallow, with falls about 80 cm depth, and moderately slow current. It is a tributary of the Cuña-Pirú stream (above Salto Encantado, a fall with 40 m depth); the creek only has 700 m from its headwaters to the confluence with Cuñá-Pirú. The rocky stream bed, covered by detritus over 50% of its surface, presents small pools and glides. *Cnesterodon pirai* was especially found forming schools of juveniles and adults in pools.

Etymology: The specific epithet *pirai* derives from the Guarani words "*pirâ*", meaning fish and the diminutive "*î*", in allusion to the small size of the fishes belonging to the genus *Cnesterodon*. A noun in apposition.

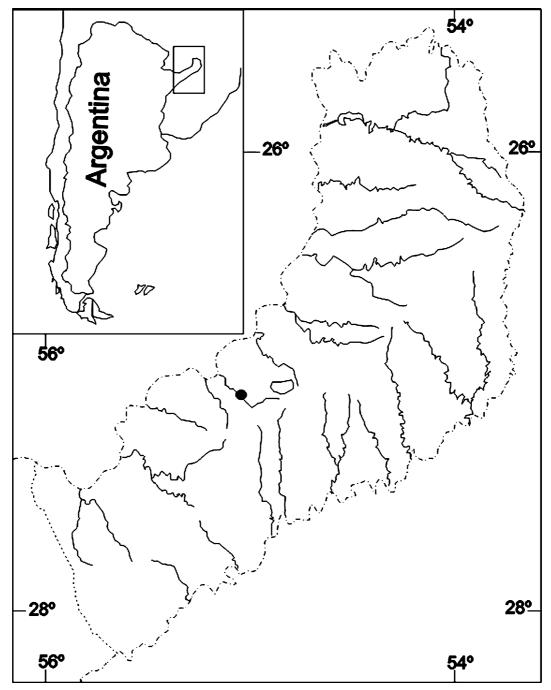


FIGURE 3. Distribution of Cnesterodon pirai. Dot indicates type locality.

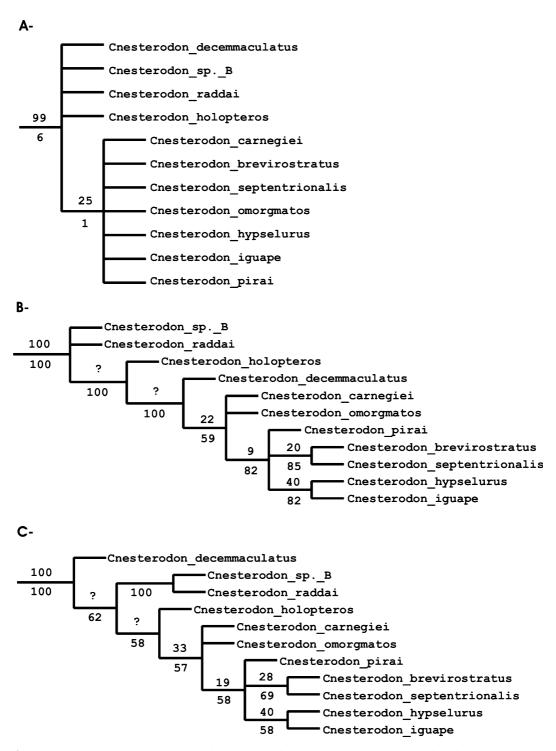


FIGURE 4. Consensus tree under a- equal weight; b- implied weighting (K=3-10); c- implied weighting (K= 11-16). The GC/relative Bremer support values are shown. Question marks in GC values represent negatives values, which are an artifact of the method, assigned to weakly supported nodes. Unsupported nodes are shown as collapsed.

Phylogenetic relationships: Codification of *Cnesterodon pirai* for the character states proposed by Lucinda & Reis (2005), characters 1 to 144, is as follows: 0023000112 1021010000 11001011011 0112030201 0210100300 003---1102 11[06][03]210102 0020200112 0010041000 1110?????0 01010???00 1100102000 0010101210 0010000001 0100. The analysis performed under equal weights produced 1938 equally most parsimonious trees, of 758 steps (CI: 0.35; RI: 0.76). The topology of consensus tree (Fig. 4 a) shows a basal polytomy formed by *Cnesterodon decemmaculatus*, *C. radai*, *C. sp. B* and *C. holopteros*. This is the sister

group of a polytomy formed by *Cnesterodon carnegiei*, *C. omorgmatos*, *C. hypselurus*, *C. iguape*, *C. brevirostratus*, *C. septentrionalis* and *C. pirai*.

Under implied weighting with concavities (K) range from 3 to 10 (Fig. 4 b) the consensus tree is partially resolved. There is a polytomy in the base of the tree formed by *Cnesterodon raddai*, *C. sp. B*, and a clade composed by the remaining species of the genus; within this clade, *C. pirai* forms a tricotomy with (*C. brevirostratus* + *C. septentrionalis*), and (*C. hypselurus* + *C. iguape*). With K from 11 to 16 (Fig. 4 c) the topology of the consensus tree varies slightly; *C. decemmaculatus* becomes basal to all other species of the genus, while the relationships of *C. pirai* remain stable.

Discussion

The arrangement of dashes in the coloration pattern, the absence of the distal filament in the gonopodium, and some measurements distinguish *Cnesterodon pirai* from other species of the genus. The presence of 6 to 8 irregular dashes on flanks, ranging from oval to irregular vertical stripes on females, and 7 to 9 irregular dashes ranging from oval to circular dots on males (dashes both on males and females covering 1 or 2 scales in transverse row, never reaching dorsal and ventral profile of body), differentiates *C. pirai* from *C. carnegiei*, *C. septentrionalis* and *C. hypselurus* (bars on body side very elongated, covering more than 4 scales in a transverse row, reaching dorsal and ventral profile of body), *C. brevirostratus* (4 to 13, usually 9 dark brown bars), *C. raddai* (1 to 4 patches of dark pigmentation along flanks), and *C. omorgmatos* (6 to 9 circular or irregular blotches or vertical wide bars along body sides). *Cnesterodon pirai* shares with *C. holopteros* the presence of 7 to 9 dark brown vertical bars, but is distinguished by the absence of small dark brown dots along predorsal portion of first, second or third lateral scale rows associated to those bars, which are present in the latter species.

The coloration pattern of the new species resembles that of *Cnesterodon decemmaculatus* (another species usually found in the lower Paraná basin) and *C. holopteros. Cnesterodon pirai* can be distinguished from *C. decemmacultaus* and *C. holopteros* by the approximately straight medial surface of ascending process of premaxilla (vs. slightly angled laterally, and angled laterally at proximal end, respectively); the presence of teeth on fourth ceratobranchial (vs. absence); and the presence of a constriction on unpaired appendix of gonopodium (vs. absence) (see Rosa & Costa, 1993: Fig. 10; Lucinda *et al.*, 2006: Fig. 4). *Cnesterodon pirai* can be further distinguished from *C. decemmaculatus* by the lack of a distal filament at tip of gonopodium and from *C. holopteros* by the free fifth gonactinost (vs. fused to complex gonactinost); and the distal portion of third and fourth gonactinosts separated except by tip of third gonactinost, which is arched backward towards gonactinost 4 (vs. completely separated).

From those species included in the same clade than *C. pirai*, the new species is differentiated from *C. hypselurus* by the absence of a longitudinal dark-brown band along flank; from *C. brevirostratus* by the presence of a pointed snout (vs. blunt snout) and a longer snout (16.7–28.7 % HL vs. 5.6–12.3 % HL); and from *C. septentrionalis* and *C. omorgmatos* by the presence of 12–13 epipleural ribs (vs. 6, and 7 or 8 epipleural ribs respectively); and from *C. iguape* by the absence of a large post-gonopodium blotch on ventral profile in adult males.

Under implied weighting for the whole concavities range, the relationships among *C. pirai*, and *C. brevirostratus*, *C. septentrionalis*, *C. hypselurus*, and *C. iguape* remain stable. The main difference between the consensus trees for K= 4 to 10 and K= 11 to 16, are produced by the different position of *C. decemmaculatus*, which does not affect the monophyly and internal relationships of the clade including *C. carnegiei*, *C. omorgmatos*, *C. pirai*, *C brevirostratus*, *C. septentrionalis*, *C. hypselurus* and *C. iguape* (Fig. 4 b and c). Also under K=11–16 the basal tricotomy is resolved, and *C. raddai* and *C. sp. B* form a monophyletic clade.

The hypothesis of relationships given here represents an advance in the present state of knowledge of the genus, but undoubtedly the discovery of new species and characters will eventually help to better understanding of the phylogeny of this genus.

Acknowledgements

We thank Miguel Rinas and Ernesto Krauczuk (Ministerio de Ecología de Misiones) for collecting permissions; park rangers of the Parque Provincial Salto Encantado for help during collecting expeditions; Jorge Williams and Guillermo Terán for help in the field; Cristina Butí for loan of collection material; Thomas Litz for donation of material of *C. holopteros*; and José Barboza Benitez and Fabio Malosch for their hospitality and conservation aims toward the area where *C. pirai* inhabits. Agencia Nacional de Promoción Científica y Tecnológica (PID 12348) funded the collecting trip; CONICET and Fundación Miguel Lillo partially supported this study. We also thank Idea Wild for the donated equipment and the Willi Hennig Society for providing TNT.

Literature cited

Aguilera, G. & Mirande, J.M. (2005) A new species of *Jenynsia* (Cyprinodontiformes: Anablepidae) from northwestern Argentina and its phylogenetic relationships. *Zootaxa*, 1096, 29–39.

Garman, S. (1895) The Cyprinodonts, Memoirs of the Museum of Comparative Zoology, 19, 1–179.

Goloboff, P.A. (1993) Estimating character weights during tree search, *Cladistics*, 9, 83–91.

Goloboff, P.A. & Farris, J.S. (2001) Methods for quick consensus estimation. Cladistics, 17, S26–S34.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2003a) *T.N.T.: Tree Analysis using New Technology*, version 1.0. Program and documentation available from the authors and at www.zmuc.dk/public/phylogeny.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003b) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.

Gosline, W.R. (1949) The sensory canals of the head in some cyprinodont fishes. with particular reference to the genus Fundulus, Occasional Papers of the Museum of Zoology – University of Michigan, 519, 1–17.

Haseman, J.D. (1911) Some new species of fishes from the Rio Iguaçu. Annals of the Carnegie Museum, 7, 374-387.

Jenyns, L. (1842) Fish. *In*: Darwin, C. *The Zoology of the Voyage of H.M.S. Beagle during the Years 1832-1836. Part 4.* Smith, Elder and Co., London, 178 pp.

Lucinda, P.H.F. (2003) Family Poeciliidae. In: Reis, R. E., Kullander, S. O. & Ferraris Jr., C. J. (Eds.). *Check list of the freshwater fishes of South and Central America* Edipucrs. Porto Alegre, pp. 555–581.

Lucinda, P.H.F., Litz, T. & Recuero, R. (2006) *Cnesterodon holopteros* (Cyprinodontiformes: Poeciliidae: Poeciliinae), a new species from the Republic of Uruguay. *Zootaxa* 1350, 21–31.

Lucinda, P.H.F. (2005) Systematics of the genus *Cnesterodon* Garman, 1895 (Cyprinodontiformes: Poeciliidae: Poecillinae). *Neotropical Ichthyology*, 3, 259–270.

Lucinda, P.H.F. & Reis, R.E. (2005) Systematics of the subfamily Poeciliinae Bonaparte (Cyprinodontiformes: Poeciliidae). *Neotropical Ichthyology*, 3, 1–60.

Parenti, L.R. (1981) A phylogenetic and biogeographical analysis of Cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bulletin of the American Museum of Natural History*, 168, 341–557.

Rosa, R.S. & Costa, W.J.E.M. (1993) Systematic revision of the genus *Cnesterodon* (Cyprinodontiformes, Poeciliidae) with the description of two new species from Brazil. *Copeia*, 1993, 696–708.

Rosen, D.E. & Mendelson, J.R. (1960) The sensory canals of head in Poeciliid fishes (Cyprinodontiformes), with reference to dentitional types. *Copeia*, 1960, 203–210.

Taylor, W.R. & Van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.

Wilcox, D., Dove, B., McDavis, D. & Green, D. (2002) UTHSCSA ImageTool Version 3.0. Available from http://ddsdx.uthscsa.edu/dig/download.html.