Papéis Avulsos de Zoologia

Museu de Zoologia da Universidade de São Paulo

Volume 53(10):129-144, 2013

www.mz.usp.br/publicacoes http://portal.revistasusp.sibi.usp.br www.scielo.br/paz ISSN impresso: 0031-1049 ISSN on-line: 1807-0205

Two new species and a review of the inseminating freshwater fish genus *Monotocheirodon* (Characiformes: Characidae) from Peru and Bolivia

Naércio A.Menezes¹
Stanley H. Weitzman²
Irani Quagio-Grassiotto³

ABSTRACT

Two new species of inseminating freshwater fishes of the genus Monotocheirodon, family Characidae, are described from Peru. Males and females of both new species have an external, visually obvious urogenital papilla that was not detected in the females in previous studies, with this longer in males, which use it as an inseminating organ. A third inseminating species from Bolivia, Monotocheirodon pearsoni, unstudied in any detail since its original description in 1924, is redescribed. This latter species lacks an inseminating organ. Monotocheirodon is redescribed, its phylogenetic relationships are briefly discussed and it is suggested that it is possibly related to the stevardiin genera Ceratobranchia, Othonocheirodus, and Odontostoechus.

KEY-WORDS: Inseminating characid fishes, new species and relationships of *Monotocheirodon*.

INTRODUCTION

Eigenmann and Pearson in Pearson (1924: 34) briefly described a new characid genus, *Monotocheirodon*, with its single new species, *M. pearsoni* described by Eigenmann in the same paper (pp. 34-35). Eigenmann and Pearson stated that *Montocheirodon* was allied to "*Cheirodon* and *Odontostilbe*," genera then assigned to the characid subfamily Cheirodontinae. Although Eigenmann did not specifically relate his new genus and species to *Creagrutus* Günther in his species description, he remarked that it had the "general appearance of *Creagrutus*." Géry (1977: 546-547)

maintained *Montocheirodon* in the Cheirodontinae and although he considered the subfamily an "unnatural group," he considered *Monotocheirodon* to be a cheirodontine "in the strict sense." Further, Géry considered *Othonocheirodus* and *Monotocheirodon* to be "adaptations from some *Odontostilbe*-like species." Malabarba (1998: 231) in a detailed phylogenetic revision of the Cheirodontinae removed *Monotocheirodon, Othonocheirodus* and 54 other genera from that subfamily to *incertae sedis* in the Characidae. Malabarba & Weitzman (2003: 73-88) in a phylogenetic study of inseminating and related non-inseminating characids placed *Montocheirodon, Othonocheirodus*,

^{1.} Museu de Zoologia, Universidade de São Paulo. Caixa Postal 42.494, 04218-970, São Paulo, SP, Brasil. E-mail: naercio@usp.br

Division of Fishes, Department of Zoology, National Museum of Natural History, MRC 0159, PO Box 37012, Smithsonian Institution, Washington, D.C. 200013-7012, USA. E-mail: weitzmas@si.edu

^{3.} Universidade Estadual Paulista, Instituto de Biociências, Departamento de Morfologia, Caixa Postal 510, CEP 18618-000,

Universidade Estadual Paulista, Instituto de Biociências, Departamento de Morfologia, Caixa Postal 510, CEP 18618-000, Botucatu, SP, Brasil.

Odontostoechus and many other characid genera, both inseminating and non-inseminating, in a new characid subgroup they called Clade A. Weitzman et al. (2005) in a discussion of inseminating characids associated with the inseminating characid subfamilies Stevardiinae and Glandulocaudinae found all three described species of Montocheirodon to be inseminating and included them in a subgroup within Clade A consisting of genera with inseminating species. Mirande (2010) proposed that the members of Clade A characids along with a few additional characid genera were a monophyletic group which he named subfamily Stevardiinae. Their phylogenetic relationships were not resolved and as emphasized by Ferreira et al. (2011) were depicted as forming a large polytomy. This subfamily was also utilized as the representative taxon of Clade A characids along with Markiana nigripinnis analyzed in a recent molecular study (Oliveira et al., 2011). The present contribution is designed to describe the two new species of Monotocheirodon, redefine this genus, and briefly discuss its relationships with the other members of the subfamily Stevardiinae.

MATERIAL AND METHODS

Count and measurement techniques are those described by Fink & Weitzman (1974: 1-2) and Menezes & Weitzman (2009: 296-297), except for the number of longitudinal scale rows below the lateral line which are counted from the pelvic-fin origin to the lateral line. In the descriptions, the range of meristic characters is presented first, followed by the mean of the sample and by counts of the holotypes and the lectotype in parentheses and total number of specimens counted. Measurements in all the tables, other than standard length (SL), are expressed as a percentage of SL except for subunits of the head that are presented as a percentage of head length. Total vertebral counts were taken from radiographs. These include the vertebrae of the Weberian apparatus as well as the complex caudal ossification, PU1 + U1 with the associated hypural bones and "half vertebrae" counted as one element. Meristic characters are presented in the description of the species. Tukey box plots were not used herein because no significant meristic differences were found among the species studied. Analyses for differences between sexes using regressions were not performed due to the very limited number of male specimens of the three species. Basic descriptive statistics were prepared using BioEstat 5.0, in Ayres et al. (2007). A difference was considered significant when $p \le 0.05$.

All mature specimens of the species of *Monoto-cheirodon* were identified to sex by examination of their gonads. In most cases tissue samples for histology were taken only from particular organs. For example, in the case of the gonads, one entire gonad was removed from one side only, usually the right side.

For Transmission Electron Microscope (TEM) preparations the gonads were extracted from specimens previously fixed in a 10% formalin solution and preserved in 70% ethanol. Fragments of gonads were post-fixed for 48 h in solutions of 2% glutaraldehyde and 4% paraformaldehyde in 0.1 M Sorensen phosphate buffer, pH 7.4. The material was post-fixed again for 2 h in the dark in 1% osmium tetroxide in the same buffer, stained in block with a aqueous solution of 5% uranyl acetate for 2 h, dehydrated in acetone, embedded in araldite, and sectioned and stained with a saturated solution of uranyl acetate in 50% ethanol and with lead citrate (Reynolds, 1963).

The following abbreviations are used for institutions: Academy of Natural Sciences, Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS); Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima (MUSM); Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (MCP); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); and National Museum of Natural History, Smithsonian Institution, Washington, D.C (USNM and NMNH).

Abbreviations in the text are: SL (standard length) and HL (head length).

RESULTS

Family Characidae Agassiz, 1844 Monotocheirodon Eigenmann & Pearson, 1924

Monotocheirodon Eigenmann & Pearson, 1924: 34 (type species: Monotocheirodon pearsoni, by monotypy).

Diagnosis: The characters listed below in combination distinguish *Monotocheirodon* from the remaining members of the subfamily Stevardiinae (*sensu* Mirande, 2010 and Oliveira *et al.*, 2011). This genus has not been included in previous phylogenetic analyses of characters involving stevardiin genera, but preliminary examination of most genera of the subfamily indicates that only character 1 in the list below is autapomorphic for *Monotocheirodon*. The remaining

characters, although useful for distinguishing *Monoto-cheirodon* are not unique to the genus.

- 1 One enlarged scale on basal portion of each caudal-fin lobe (Figs. 1, 9, and 12).
- 2 Two rows (one external and one internal) of short and slender gill-rakers present on each branchial arch (Fig. 13).
- 3 Single row of four distally compressed, pedunculate, and multicuspid teeth present on the premaxilla (Figs. 2, 10, and 14).
- 4 Ascending process of the premaxilla strongly bent ventrally (Figs. 2, 10, and 14).
- 5 Posterior portion of maxilla strongly bent ventrally (Figs. 2, 10, and 14).
- 6 Anterior dentary teeth not notably larger than the remaining teeth on the bone. All dentary teeth gradually decreasing in size posteriorly (Figs. 2, 10, and 14)
- 7 Two or three longitudinal scale rows from lateral line to pelvic-fin origin (Figs. 1, 9, and 12).
- 8 Adipose fin absent (Figs. 1, 9, and 12).
- 9 Anal fin short, with 8-12 branched rays (Figs. 1, 9, and 12).
- 10 Hooks absent on pelvic and anal fins of males (Figs. 5 and 6).

Key to the species of Monotocheirodon

- Premaxillary teeth with 5 cusps in adult males and females (Fig. 10); dorsal-fin height 16.1-17.8% of SL in females and juveniles, 18-18.7 in males (Table 2); urogenital papilla of adult sexually active males short about twice length of anal-fin base (Fig. 9)

Monotocheirodon pearsoni Eigenmann, 1924 Figs. 1, 2, 5, 6, Table 1

Monotocheirodon pearsoni Eigenmann, in Pearson, 1924: 34, pl. 11, fig. 1 (original description, type locality: Bolivia, Espia, Beni river basin). Malabarba, 1998: 200 (structure of pseudotympanum). Malabarba & Weitzman, 2000: 269-283 (insemination). Lima et al., 2003: 150 (maximum length; distribution; remarks and references). Weitzman et al., 2005: 357 (listed in comparative specimens examined).

Specimens examined: All specimens from Bolivia.

Lectotype: CAS 59792 (SL 35.5 mm), Río Beni basin, confluence of Ríos La Paz and Miquilla where they form Río Bopi near Espia, 16°33'S, 67°51'W.

Paralectotypes: CAS 233970 (6, SL 19.5-29.1), UMMZ 66484 (4, SL 23.5-29.2), collected with lectotype; UMMZ 66485 (5, SL 23-27.8 mm), Río Iniqui (exact coordinates not found).

Diagnosis: Monocheirodon pearsoni can be easily distinguished lacking the externally visible urogenital papilla present in males and females of *M. drilos* and *M. kontos* (see Figs. 1, 9, and 12). Aditionally it has a smaller horizontal eye diameter (13.5-16.6% of HL) than its congeners (18.3-22.6% in *M. drilos* and 18.0-21.6% in *M. kontos*).

Description: Morphometric data of lectotype and paralectotypes presented in Table 1. Stevardiine characid reaching at least 35.5 mm SL. Body cylindrical in cross section; greatest depth situated between verticals through tip of pectoral fin and dorsal-fin origin. Dorsal profile of head anterior to nape slightly convex to snout region dorsal to nostril. Snout bluntly convex with tip at about level of horizontal through mid-point of orbit. Lower jaw margin convex with jaw somewhat included below upper jaw. Ventral profile of head gently convex, continuous with gently convex abdominal region extending to anal-fin origin. Body profile along anal-fin base approximately straight to slightly convex to posterior termination of anal fin. Ventral profile of caudal peduncle almost straight. Dorsal profile of body between nape and dorsal-fin origin gently convex. Base of dorsal fin slightly convex and somewhat inclined posteroventrally. Body profile between termination of base of dorsal fin and caudal-fin base slightly concave.

Two unbranched dorsal-fin rays in all specimens, branched rays 7-8, 7.5, (7), n = 17, SD = 0.5;

TABLE 1: Morphometrics of *Monotocheirodon pearsoni*. Standard length expressed in mm; measurements through headd length are percentages of standard length; the last four entries are percentages of head length. Specimens are from CAS 59792 (lectotype), 233970 (paralectotypes); UMMZ 66484 (syntypes), 66485.

			N	Aales			Females and juveniles			
Characters	Lectotype	n	range	mean	SD	n	range	mean	SD	
Standard length	35.5	2	25.5-29.1	27.3	2.50	14	19.5-35.5	26.0	4.0	
Depth at dorsal-fin origin	21.1	2	18.8-20.0	19.3	0.80	14	18.0-23.0	20.6	1.7	
Snout to dorsal-fin origin	53.5	2	51.5-53.3	52.4	1.20	14	52.1-55.4	54.1	1.1	
Snout to pectoral-fin origin	18.3	2	21.5-22.3	22.0	0.50	14	18.3-21.7	20.4	1.0	
Snout to pelvic-fin origin	45.0	2	46.7-47.0	46.9	0.20	14	44.1-48.6	46.4	1.4	
Snout to anal-fin origin	62.5	2	60.8-61.8	61.3	0.70	14	59.1-65.0	62.5	1.6	
Caudal peduncle depth	10.1	2	09.0-10.0	09.5	0.60	14	08.2-11.0	09.6	1.0	
Caudal peduncle length	22.0	2	19.6-21.6	20.1	0.70	14	19.1-22.7	20.8	1.0	
Pectoral-fin length	18.8	2	18.8-19.0	18.8	0.05	14	17.4-19.8	18.7	0.7	
Pelvic-fin length	14.3	2	13.7-20.6	17.1	4.87	14	10.8-14.7	13.0	1.2	
Dorsal-fin base length	09.3	2	09.6-09.8	09.7	0.12	14	07.5-10.2	09.0	0.9	
Dorsal-fin height	14.1	2	13.0-20.0	16.4	4.94	13	12.6-16.3	14.6	1.3	
Anal-fin base length	12.6	2	10.0-12.0	11.0	1.57	14	09.3-12.7	10.7	1.0	
Anal-fin lobe length	13.5	2	15.0-17.2	16.0	1.61	14	10.6-13.6	12.3	0.9	
Eye to dorsal-fin origin	14.8	2	41.5-42.0	41.7	0.25	14	40.6-43.8	42.4	1.2	
Dorsal-fin origin to caudal-fin base	44.2	2	44.6-45.0	44.8	0.30	14	42.8-46.4	44.4	1.1	
Bony head length	19.7	2	21.1-22.3	21.7	0.82	14	19.7-22.2	21.2	0.6	
Horizontal eye diameter	15.7	2	14.8-15.4	15.1	0.40	14	13.5-16.6	15.0	1.0	
Snout length	17.1	2	15.4-16.6	16.0	0.90	14	13.3-17.3	15.5	1.2	
Least interorbital width	25.7	2	24.6-26.0	25.2	0.92	14	21.6 -26.1	24.2	1.4	
Upper jaw length	28.5	2	26.0-27.7	26.8	1.24	14	25.0-30.0	27.1	1.5	

posterior ray not split to its base. Dorsal-fin height apparently sexually dimorphic (see discussion under sexual dimorphism). Adipose fin absent. Unbranched anal-fin rays ii or iii, usually ii; branched rays 8-10, 9.5, (10), n = 17, SD = 0.6; posterior ray split to its base and counted as one ray. No hooks on anal fin of males (Fig. 5). Pectoral-fin rays i, 8-10, 9, (9), n = 17, SD = 0.4. Tip of pectoral fin falling short of pelvic-fin origin. Pectoral-fin rays lacking hooks. Pelvic-fin rays i, 5, i, n = 17. Sexually active males without pelvic-fin hooks (Fig. 6). Pelvic-fin length of sexually mature specimens apparently sexually dimorphic (see discussion under sexual dimorphism). Principal caudal-fin rays 10/9 in all specimens.

Scales cycloid: Lateral line complete; perforated scales 32-38, 35.1, (36), n = 14, SD = 1.5. Predorsal scales 13-17, 16, (13), n = 16, SD = 1.0. Scale rows between dorsal-fin origin and lateral line 4-5, 4.6, (5), n = 16, SD = 0.5. Scale rows from pelvic-fin origin to lateral line 2-3, 2.8, (3), n = 16, SD = 0.3. Scale rows around caudal peduncle 10 in all specimens, n = 16. Row of enlarged scales present along anal-fin base.

Premaxilla with single row of 4 multicuspid teeth (Fig. 2) in all specimens. All teeth compressed, pedunculate with wider distal parts spatulate with 6 or

7 cusps and two or three middle cusps largest. Small cusps sometimes appearing only as small rounded process. Maxillary teeth (Fig. 2) shaped like premaxillary teeth with larger anterior teeth bearing 6 or 7 cusps and smaller posterior teeth with 3 or 4 cusps. Total number of maxillary teeth 5-6, 5.7, (6), n = 16, SD = 0.5. Dentary teeth (Fig. 2) shaped like premaxillary and maxillary teeth, progressively decreasing in size posteriorly. Most dentary teeth with 5 cusps, with middle cusp usually largest. Total number of dentary teeth 7-9, 8.1, (8), n = 17, SD = 0.5.

Vertebrae 36-38, 37.1, n = 12, SD = 0.7. Dorsal limb gill rakers 8-10, 8.8, (8) n = 15, SD = 0.8; ventral limb gill rakers 11-15, 12.4, (12) n = 17, SD = 1.1. Branchiostegal rays 4 in one cleared and stained specimen, 3 rays originating on anterior and one on posterior ceratohyal.

Color in alcohol: Pigmentation comparable in both sexes. Overall body color pale to yellowish-brown. Dark chromatophores widespread over all of body, more condensed dorsally and slightly darker in that region than on ventral part of body. Dark roundish humeral blotch situated above anterior portion of pectoral fin and about two scales distant from posterodorsal part of opercle. Dark longitudinal stripe extending on



FIGURE 1: Monotocheirodon pearsoni, CAS 59792, adult male above, 29.4 mm SL and adult female below, 35.5 mm SL.

body from posterior border of blotch to base of median caudal-fin rays. Stripe anteriorly narrower from posterior border of humeral blotch to point ventral to middle of dorsal-fin base and wider from this point to caudal-fin base. Terminal portion of stripe darker on caudal peduncle, forming inconspicuous dark spot.

FIGURE 2: *Monotocheirodon pearsoni,* UMMZ 66485 (upper jaw), C&S, female, 26.3 mm SL, CAS 5792 (lower jaw), male, 29.4 mm SL, dentition, lateral view, left side, anterior at left.

Head darker dorsally and on anterior portion of snout; lighter and with scattered dark chromatophores on region anterior to eye, infraorbitals, central portion of opercular area and lower jaw. Enalged scales on base of each caudal-fin lobe with scattered dark chromatophores. All fins hyaline with scattered dark chromatophores.

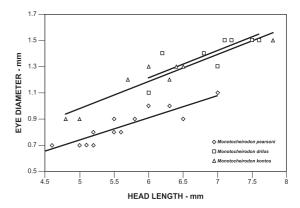


FIGURE 3: Eye diameter as function of head length for species of *Monotocheirodon.*

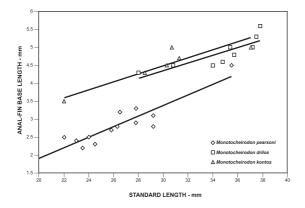


FIGURE 4: Anal-fin base length as function of standard length for species of *Monotocheirodon*.

Sexual dimorphism: Means corresponding to pelvicfin length and dorsal-fin height differ considerably between males and females (Table 1), but tests to evaluate if such differences would be statistically significant are meaningless since only two males are available.

Reproductive mode and gonad anatomy: Histological analysis revealed the presence of spermatozoa

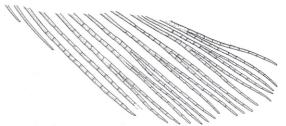


FIGURE 5: Monotocheirodon pearsoni, CAS 59792, C&S, male, 29.4 mm SL; anal-fin rays, lateral view, left side.

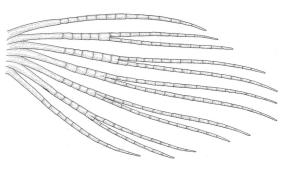


FIGURE 6: Monotocheirodon pearsoni, CAS 59792, C&S, male, 29.4 mm SL; pelvic-fin rays, ventral view, left side.

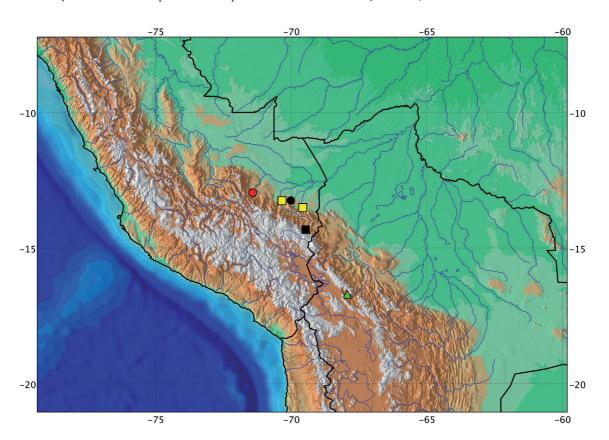


FIGURE 7: Map of western South America showing collecting sites and type localities (black symbols) of species of *Monotocheirodon*. Squares: *Monotocheirodon kontos*; circles: *M. drilos*; triangle: *M. pearsoni*. Some symbols may represent more than one locality.

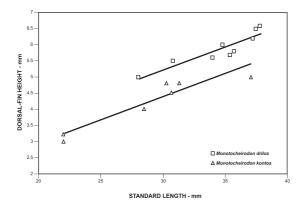


FIGURE 8: Dorsal-fin height as function of standard length for Monotocheirodon drilos and M. kontos.

with spherical nuclei in ovaries from one mature female of *Monotocheirodon pearsoni* (Burns & Weitzman, 2006, fig. 1, Table 1). This indicates that the species can be classified as "aquasperm", characteristic of externally fertilizing characids and is inseminating.

Distribution: Monotocheirodon pearsoni is known from headwaters of the Río Bopi, Río Beni basin and Río Iniqui (not exactly located), Bolivia, at about 5,000 m of elevation (Fig. 7).

Monotocheirodon drilos, new species Figs. 9-11, Table 2

Monotocheirodon sp. – Weitzman et al., 2005: 357, Burns & Weitzman, 2006: 529-530 (MUSM 11082, ANSP 143791, 143792).

Specimens examined: All specimens from Peru.

Holotype: MUSM 41541, male, SL 33.3 mm, Sandia, Zona Reservada Tambopata-Candamo, stream Ebebahuaeji (empties into Río Candamo), 13°14'56.4"S, 70°00'34.5"W, 31 March 1997, Fonchii Chang.

Paratypes: MUSM 11082, 2 (SL 28 and 32 mm), USNM 405296, 2 (31.8 and 34.8 mm) collected with holotype. ANSP 143790, 1 (SL 37.2 mm), Río Shintuya at Shintuya (exact coordinates not found). ANSP 143792, 6 (SL 300.8-37.8), border between Departamento of Cuzco and Departamento of Madre de Dios, Río Carbón (empties into Río Madre de Dios), 12°53'S, 71°20'W.

Diagnosis: Males and females of Monotocheirodon drilos have an externally visible urogenital papilla which is absent in M. pearsoni. The urogenital papilla

TABLE 2: Morphometrics of *Monotocheirodon drilos*. Standard length expressed in mm; measurements through head length are percentages of standard legth; the last four entries are percentages of head length. Specimens are from MUSM 41541 (holotype), 11082 (paratypes); ANSP 143790, 143792 (paratypes). Values of **p** in bold indicates significant statistical differences.

Characters	Holotype	n	Males		CD		Females and juveniles		CD	
			range	mean	- SD	n	range	mean	SD	p value
Standard length	33.3	3	31.8-33.3	32,3	0.81	9	28.0-37.8	34.5	3.2	
Depth at dorsal-fin origin	22.5	3	21.8-23.0	22.4	0.54	9	21.4-23.5	22.2	0.7	0.4055
Snout to dorsal-fin origin	52.0	3	51.0-52.0	51.5	0.51	9	50.6-53.7	52.4	1.1	0.2294
Snout to pectoral-fin origin	19.5	3	19.5-20.0	19.7	0.24	9	17.2-20.4	19.4	1.0	0.9263
Snout to pelvic-fin origin	44.1	3	44.1-45.3	44.7	0.58	9	43.1-47.6	45.7	1.3	0.1655
Snout to anal-fin origin	57.0	3	57.0-58.7	58.1	0.91	9	57.0-61.4	59.6	2.0	0.1655
Caudal peduncle depth	10.8	3	10.8-11.0	10.9	0.99	9	00.9-10.7	10.1	0.6	0.0126
Caudal peduncle length	21.0	3	21.0-21.8	21.5	0.45	9	20.6-22.8	21.4	0.6	0.6439
Pectoral-fin length	19.5	3	19.5-20.3	19.7	0.46	9	17.0-19.6	18.1	0.8	0.0335
Pelvic-fin length	16.5	3	16.5-16.8	16.7	0.18	8	12.4-13.0	12.6	0.2	0.0100
Dorsal-fin base length	09.0	3	08.8-09.3	09.1	0.28	9	08.2-10.0	09.2	0.5	0.6439
Dorsal-fin height	18.0	3	18.0-18.7	18.3	0.37	9	16.1-17.8	17.0	0.7	0.0126
Anal-fin base length	15.0	3	13.8-15.0	14.3	0.62	9	13.2-15.3	14.0	0.7	0.6439
Anal-fin lobe length	14.4	3	14.4-14.7	14.6	0.14	9	13.3-15.6	14.5	0.7	0.7815
Eye to dorsal-fin origin	39.6	3	39.6-40.8	40.4	0.65	9	40.2-42.4	41.5	0.7	0.0790
Dorsal-fin origin to caudal-fin base	49.5	3	49.5-51.5	50.9	1.16	9	47.0-50.0	48.2	1.0	0.0208
Bony head length	20.1	3	19.8-20.3	20.1	0.25	9	19.5-21.4	20.3	0.5	0.6439
Horizontal eye diameter	21.0	3	19.0-21.0	20.0	0.90	9	18.3-22.6	20.3	1.3	0.7115
Snout length	16.4	3	15.8-17.0	16.4	0.52	9	16.1-19.7	18.0	1.1	0.0522
Least interorbital width	26.8	3	26.8-28.5	27.7	0.85	9	26.6-29.0	27.4	0.7	0.5175
Upper jaw length	32.8	3	31.7 -32.8	32.3	0.54	9	30.0-33.8	32.3	1.3	0.6439

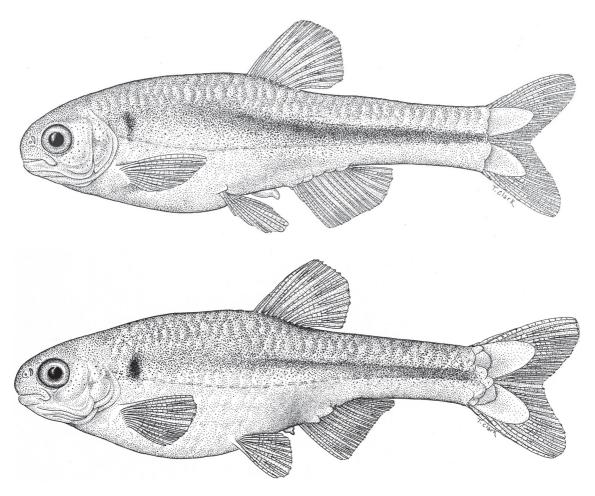


FIGURE 9: Monotocheirodon drilos, MUSM 11082, adult male above, 33.6 mm SL and adult female, below, 33.0 mm SL.

of sexually active males of *M. drilos* is shorter (half length of anal-fin base *versus* about equal to length of anal fin-base in *M. kontos*). Females and juveniles of

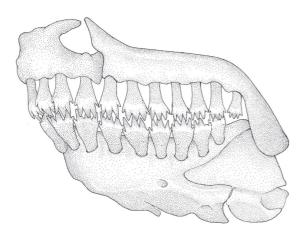


FIGURE 10: Monotocheirodon drilos, MUSM 11082, C&S, adult male, 43.5 mm SL; jaws and dentition, lateral view, left side, anterior at left.

M. drilos and M. kontos can be differentiated in the height of the dorsal fin (16.1-17.8% SL in M. drilos versus 13.4-15.8% SL in M. kontos). The number of premaxillary tooth cusps (5 in M. drilos vs 7 in M. kontos) is also useful to distinguish adult males and females of both species (Figs. 10 and 14).

Description: Morphometric data of holotype and paratypes presented in Table 2. Stevardiine characid reaching at least 37.8 mm SL. Body cylindrical in cross section; greatest body depth between verticals through middle and tip of pectoral fin. Dorsal profile of head anterior to nape strongly convex to snout region in males, less so in females. Snout bluntly convex; tip of snout at about horizontal through mid-point of orbit. Lower jaw convex in profile and somewhat included below upper jaw. Ventral profile of head gently convex, and continuous with strongly convex abdominal region as far as anal-fin origin. Body profile along anal-fin base approximately straight to slightly convex to posterior termination of anal fin. Ventral profile

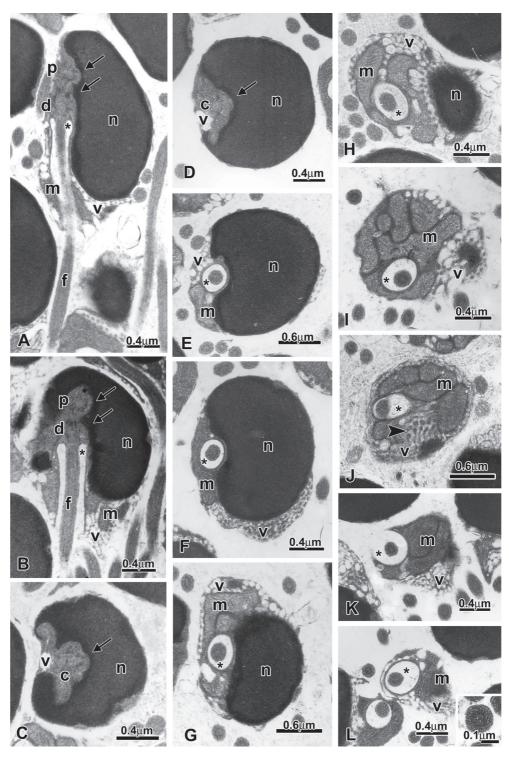


FIGURE 11: Spermatozoa of *Monotocheirodon drilos* (ANSP 143791, 33.9 mm SL). A, B: Longitudinal section of spermatozoa. Note lateral position of nucleus (n) in relation to flagellar axis and nuclear fossa (double arrow) near tip of nucleus; short midpiece contains cytoplasmic canal (asterisks) that houses initial segment of flagellum (f), mitochondria (m) that increase in number from tip of base of nucleus and several vesicles (v). Proximal centriole (p) inside first concavity of fossa and distal centriole (d) outside. C-H: Cross sections at different levels of nucleus showing branched format of first concavity of nuclear fossa (arrow), cytoplasmic canal (c) and initial segment of flagellum (f) running along nuclear outline. I-L: Cross sections at different levels of midpiece displaying mitochondria (m) concentrated mainly at base of nucleus and decreasing progressively along midpiece. Cytoplasm of midpiece filled by vesicular system (v). Electron dense dots (arrowhead) indicate connections of vesicles.

of caudal peduncle slightly convex. Dorsal profile of body between nape and dorsal-fin origin gently convex. Base of dorsal fin slightly convex and somewhat inclined posteroventrally. Body profile between posterior terminus of dorsal fin and caudal-fin base slightly convex in males and almost straight in females.

Unbranched dorsal-fin rays 2 in all specimens, branched rays 7-8, 7.1, (7) n = 12, SD = 0.4); posterior ray not split to its base. Dorsal-fin height apparently sexually dimorphic (see discussion under sexual dimorphism). Adipose fin absent. Unbranched analfin rays ii in all specimens; branched rays 9-12, 10, (9), n = 12, SD = 0.9; posterior ray split to its base and counted as one ray. No hooks on anal fin of males. Pectoral-fin rays i, 9-10, 9.1, (9), n = 12, SD = 0.6. Pectoral fin longer in mature males, with tip almost reaching pelvic-fin origin; shorter in immatures and females, with tip distant from pelvic-fin origin. Pectoral-fin rays without hooks. Pelvic fin with one anterior and one posterior unbranched ray, and branched rays 4-5, 4.7, (7) n = 12, SD = 0.4. Sexually active males lacking pelvic-fin hooks. Pelvic-fin length of sexually mature specimens sexually dimorphic (see discussion under sexual dimorphism). Principal caudal-fin rays 10/9 in all specimens.

Scales cycloid: Lateral line complete, perforated scales 33-39, 36.8, (33), n = 12, SD = 1.9. Predoral scales 13-15, 14.5, (14), n = 12, SD = 0.7. Scale rows between dorsal-fin origin and lateral line 4-5, 4.5, (5), n = 12, SD = 0.5. Scale rows from pelvic-fin origin to lateral line 3, n = 12. Scale rows around caudal peduncle 10 in all specimens, n = 12. Row of enlarged scales present along anal-fin base.

Premaxilla with single row of 4 multicuspid teeth (Fig. 10) in all specimens. All teeth compressed, pedunculate with distal parts spatulate with 5 cusps; three middle cusps largest, and marginal cusps reduced. Maxillary teeth (Fig. 10) identical in form to premaxillary teeth, also with 5 cusps, but with three middle cusps slightly smaller than those of premaxillary teeth. Total number of maxillary teeth (Fig. 10) identical to premaxillary and maxillary teeth, with 3 large middle cusps and reduced marginal cusps. Total number of dentary teeth 8-11, 9.3, (9), n = 12, SD = 0.4.

Vertebrae 37-38, 37.7, n = 8, SD = 0.4. Dorsal limb gill rakers 9-10, 9.3, (9), n = 11, SD = 0.4; ventral limb gill rakers 11-15, 13.6, (12), n = 11, SD = 0.4. Branchiostegal rays 4 in one cleared and stained specimen; 3 rays originating on anterior and one on posterior ceratohyal.

Color in alcohol: Background body color pale to yellowish brown, darker dorsally due to presence of dark chromatophores largely concentrated towards posterior border of scales. Dark chromatophores fewer on posterior border of scales of midlateral and ventral parts of body. Dark longitudinal dark stripe extends from posterodorsal part of opercle to caudal-fin base. Stripe anteriorly inconspicuous and slightly arched dorsally from upper part of opercle to point below dorsal-fin origin; bordered ventrally by lateral line. Stripe more conspicuous and wider from point above anal-fin origin to caudal-fin base. Dark vertically elongate humeral blotch, located about two scales posterior of posterodorsal portion of opercle, and extending one scale ventral of lateral line.

Head darker on upper part of snout and area dorsal to eye with scattered dark chromatophores on ventral portion of infraorbital bones and opercular region. Urogenital papilla and all fins with scattered dark chromatophores. Large scales on basal portion of each caudal-fin lobe with dark chromatophores mostly concentrated on their basal and median portions.

Sexual dimorphism: The *p* value in Table 2 suggests that the caudal peduncle depth, pectoral-fin length, pelvic-fin length, dorsal-fin height and the distance from dorsal-fin origin to caudal-fin base are sexually dimorphic. Regression data to test the differences more accurately were not used due to the limited number available mature males.

Reproductive mode and gonad anatomy: Males of Monotocheirodon drilos (MUSM 11082, ANSP 143791 and 143792) identified as Monotocheirodon sp. were used by Burns & Weitzman (2006) for histological sections of the urogenital papilla, which was characterized as a large intromittent organ used for insemination of the females. The sperm was found to have elongate nuclei 1.8-2.1 μ m in length, usually characteristic of inseminating and internally fertilizing fishes.

Examination of sperm cell ultrastructure using TEM confirmed that the nucleus is elongate in the direction of the flagellar axis (Fig. 11, A-G) and is approximately 2.05 μm in length (SD \pm 0.2 μm). It contains highly condensed granular chromatin and in cross section shows a concave outline (Fig. 11, A-F). In the centriolar complex, the centrioles are perpendicular to one another (Fig. 11, A-B). The mitochondria and a well-developed vesicular system surround the cytoplasmatic canal for its entire dimension (Fig. 11, E-L). The flagellum originates at about the middle of the nuclear length (Fig. 11, A-B). The midpiece is conical,

strongly asymmetric (Fig. 11, A-B) and 0.6 μm in length (SD \pm 0.1 μm). A single flagellum emerges from the midpiece (Fig. 1 I-L).

Etymology: The name drilos is Greek masculine meaning penis. The word is used here in reference to the prominent male inseminating organ. A noun in apposition.

Distribution: This species is known from headwaters of Ríos Tambopata and Madre de Dios, Río Madre de Dios basin, Peru (Fig. 7).

Monotocheirodon kontos, new species Figs. 12-15, Table 3

Monotocheirodon sp. – Burns & Weitzman,
2006: 529-530 (MUSM 6756 and 11250).
Monotocheirodon personi [sic] – Ferreira et al. 2011 (misidentification; MUSM 11416, listed in comparative material).

Specimens examined: All specimens from Peru.

Holotype: MUSM 41542, male, SL 33.5 mm, Río Inambari, Sandia, Muspaypampa, 14°14'41"S, 69°25'51"W, 6 July 1994, Fonchii Chang.

Paratypes: MUSM 6756 (4, SL 22-37.1 mm) collected with holotype. MUSM 11644 (2, SL 30.7 and 31.3 mm), Ouno, Sandia, Zona Reservada Tambopata-Candamo, cuenca Ebebahuaeji, 13°24′ 52″S, 70°00′48″W. MUSM 11250 (4, SL 24.5-31.3 mm), USNM 405297 (2, SL 26.8 and 28.5 mm), Río Malinowski (empties into Rio Madre de Dios), Zona Reservada Tambopata-Candamo, 13°08′00″S, 70°17′00″W.

Diagnosis: M. kontos has a urogenital papilla in sexually active males and females which is absent in M. pearsoni. The urogenital papilla in M. kontos is about equal length of anal-fin base versus half length of anal-fin base in M. drilos. Females and juveniles of M. kontos and M. drilos can be distinguished in the height

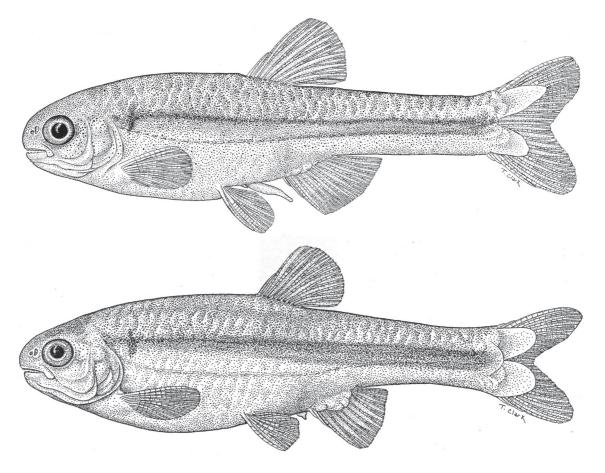


FIGURE 12: Monotocheirodon kontos, MUSM 6756, adult male above, 36.7 mm SL and adult females, 33.7 mm SL.

TABLE 3: Morphometrics of Monotocheirodon kontos. Standard length expressed in mm; measurements through head length are percent-
ages of standard length; the last four entries are percentages of head length. Specimens are from MUSM 41542 (holotype), 6756, 11250,
11644 (paratypes); USNM 405297 (paratypes). Values of p in bold indicates significant statistical differences

Characters	Holotype	n	Males		CD.		Females and juveniles		CD.	
			range	mean	- SD	n	range	mean	SD	p value
Standard length	33.5	5	24.0-33.5	27.2	3.7	8	22.0-37.1	29.1	5.0	
Depth at dorsal-fin origin	20.0	5	20.0 -21.8	20.8	0.6	8	19.6-24.0	21.6	1.6	0.6084
Snout to dorsal-fin origin	52.5	5	52.2-53.4	52.8	0.5	8	51.2-54.5	52.6	1.0	0.6606
Snout to pectoral-fin origin	20.9	5	18.3-21.0	19.6	1.0	8	18.1-20.4	19.1	0.9	0.3798
Snout to pelvic-fin origin	45.6	5	44.7-46.5	45.5	0.7	8	43.1-47.1	45.1	1.3	0.4642
Snout to anal-fin origin	58.0	5	57.5-61.2	59.0	1.5	8	56.8-61.7	59.1	1.7	0.7697
Caudal peduncle depth	11.3	5	10.4-11.3	10.8	0.3	8	09.6-11.3	10.4	0.7	0.2416
Caudal peduncle length	21.5	5	19.4-21.5	20.3	1.5	8	19.0-23.0	20.5	1.5	0.7697
Pectoral-fin length	19.4	5	19.4-21.2	20.1	0.8	8	18.2-20.3	19.5	0.8	0.3798
Pelvic-fin length	15.5	5	14.5-15.5	15.0	0.8	8	10.8-13.2	12.2	0.8	0.0034
Dorsal-fin base length	07.4	5	07.4-09.0	08.3	0.5	8	08.0-08.4	08.1	0.1	0.1432
Dorsal-fin height	16.4	5	16.4-18.1	17.3	0.7	8	13.4-15.8	14.6	0.8	0.0034
Anal-fin base length	14.0	5	14.0-15.2	14.5	0.4	8	13.4-16.3	15.2	0.8	0.1073
Anal-fin lobe length	12.8	5	12.8-14.7	13.8	0.6	8	12.7-13.5	13.0	0.3	0.0192
Eye to dorsal-fin origin	41.0	5	38.7-40.9	39.7	0.7	8	37.3-40.4	39.3	1.1	0.9417
Dorsal-fin origin to caudal-fin base	47.7	5	46.6-48.3	47.7	0.6	8	45.3-49.8	47.1	1.7	0.3055
Bony head length	21.2	5	20.4-23.0	21.1	1.0	8	19.8-22.7	20.8	1.0	0.6606
Horizontal eye diameter	21.1	5	18.3-21.1	19.6	1.0	8	18.0-21.6	19.7	1.2	0.8833
Snout length	18.3	5	16.3-18.3	17.6	0.7	8	15.8-18.3	17.0	0.8	0.3055
Least interorbital width	28.1	5	26.5-28.1	27.3	0.7	8	26.0-28.2	27.1	0.8	0.9273
Upper jaw length	32.4	5	30.1-32.6	31.5	1.1	8	30.0-32.8	31.5	0.8	0.8262

of dorsal fin (13.4-15.8% of SL in the former *versus* 16.1-17.8 in the latter). The number of premaxillary tooth cusps (7 in *M. kontos versus* 5 in *M. drilos*) differentiate adult males and females of both species.

Description: Morphometrics of holotype and paratype presented in Table 3. Stevardiin characid reaching at least 37.1 mm SL. Body cylindrical in cross section; greatest body depth situated between verticals through tip of pectoral fin and dorsal-fin origin. Dorsal profile of head anterior to nape strongly convex in males, slightly convex in females to snout region dorsal to nostril. Snout bluntly convex; tip of snout situated along horizontal through approximate midpoint of orbit. Lower jaw convex in ventral profile and somewhat included below upper jaw. Ventral profile of head gently convex, continuous with gently convex in males and strongly convex abdominal region in females extending to anal-fin origin. Body profile along anal-fin base approximately straight to slightly convex to posterior termination of anal fin. Ventral profile of caudal peduncle almost straight in males, slightly convex in females. Dorsal profile of body between nape and dorsal-fin origin gently convex. Base of dorsal fin straight and somewhat inclined posteroventrally. Body profile between basal of last dorsal-fin ray and

caudal-fin rays almost straight in males, slightly concave posterodorsally in females

Unbranched dorsal-fin rays 2 in all specimens, branched rays 7-8, 7.7, (8), n = 13, SD = 0.5; posterior ray not split to its base. Dorsal-fin height sexually dimorphic (see discussion under Sexual dimorphism). Adipose fin absent. Unbranched anal-fin rays ii or iii, most usually ii; branched rays 10-11, 10.1, (10), n = 13, SD = 0.4; posterior ray split to its base and counted as one ray. No hooks present on anal fin of mature males. Pectoral-fin rays i, 8-9, 8.5, (8) n = 13, SD = 0.5. Tip of pectoral fin falling short of pelvic-fin origin. Pectoral-fin rays lacking hooks. Pelvic-fin rays i, 5, i, n = 13. Sexually active males lacking pelvic-fin hooks. Pelvic-fin length of sexually mature males sexually dimorphic (see under Sexual dimorphism). Principal caudal-fin rays 10/9 in all specimens.

Scales cycloid: Lateral line complete, perforated scales 36-38, 37.1, (37) n = 12, SD = 0.6. Predorsal scales 13-15, 14.2, (15), n = 12, SD = 0.7. Scale rows between dorsal-fin origin and lateral line 4-5, 4.6, (4), n = 12, SD = 0.5. Scale rows from pelvic-fin origin to lateral line 2-3, 2.7, (2), n = 12, SD = 0.4. Scale rows around caudal peduncle 10 in all specimens, n = 12. Row of enlarged scales along anal-fin base.

Premaxilla with single row of 4 multicuspid teeth (Fig. 14) in all 13 specimens. All teeth compressed and pedunculate with distal parts spatulate with 7 cusps in adult males and females; 3 middle cusps largest, and marginal cusps smaller. Maxillary teeth (Fig. 14) identical in form to premaxillary teeth; most teeth with 6-7 cusps, 5-8, 7.1, (7), n = 13, SD = 1. Dentary dentition identical in form to that on premaxilla and maxilla; with 3 middle cusps slightly larger than marginal cusps. Total number of dentary teeth 7-11, 8.6, 9 (13), n = 13, SD = 1.2.

Vertebrae 37-39, 37.8, (38), n = 14, SD = 0.5. Dorsal limb gill rakers 8-9, 8.4, (8), n = 13, SD = 0.5; ventral limb gill rakers 12-14, 12,7, (13), n = 13, SD = 0.7. Branchiostegal rays 4 in one cleared and stained specimen; 3 rays originating on anterior and one on posterior ceratohyal.

Color in alcohol: Identical to that of *M. drilos*, except that the head is dark overall with the central portions of maxilla, infraorbitals, preopercle, dorsal and ventral parts of opercle, subopercle and branchiostegal rays and basal portion of pectoral fin lighter with scattered dark chromatophores. Longitudinal dark stripe on body identical to that of *M. pearsoni*, but dark chromatophores are more densely concentrated along its dorsal and posterior portions.

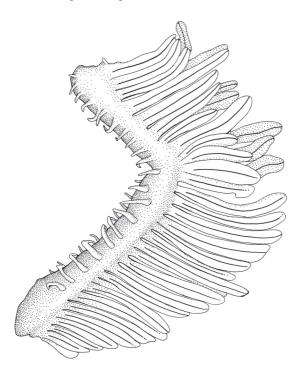


FIGURE 13: *Monotocheirodon kontos*, MUSM 11250, female, 37.1 mm SL; gill rakers on first gill arch, lateral view, left side.

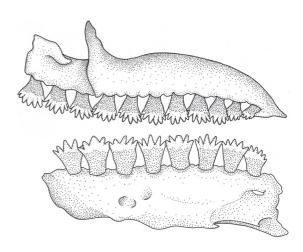


FIGURE 14: Monotocheirodon kontos, MUSM11250, C&S, female, 37.1 mm SL; jaws and dentition, lateral view, left side, anterior at left.

Sexual dimorphism: The *p* values in Table 3 indicate that pelvic-fin length, dorsal-fin height and anal-fin lobe length are sexually dimorphic, but testing these differences through regression analysis is inappropriate in light of using the limited number of available males and females.

Reproductive mode and gonad anatomy: Males and females of this species (MUSM 6756 and 11250), identified as Monotocheirodon sp. were also used by Burns & Weitzman (2006) for histological analysis of the urogenital papilla and the ovary of mature females. The results revealed that the intromittent organ of Monotocheirodon kontos, which is larger than that of M. drilos is also used to inseminate females and that the more elongate nuclei of the spermatic cells are 4.1 μm in length.

As in Monotocheirodon drilos, the sperm nucleus contains highly condensed granular chromatin, but it is more elongate toward the flagellar axis being approximately 3.95 μ m in length (SD \pm 0.4 μ m) (Fig. 15, A-F). The flagellum originates along the first quarter of the nuclear length (Fig. 15, A-B). In cross section the flagellum shows an irregular outline with depressions (Fig. 15, C-F) and in the centriolar complex the centrioles are oblique to one another (Fig. 15 B-inset). Other distinctive sperm nucleus features of *M. kontos* are: the mitochondria are elongate, display a longitudinal position relative to the flagellar axis (Fig. 15 B) and are mainly accumulated in the depressions on the nuclear outline (Fig. 15 E-F); the vesicular system is formed by a large number of small interconnected vesicles positioned very close to one another giving the system an alveolar appearance (Fig. 15, F-L); due to the superposition of the membrane, the points where the vesicles are connected are

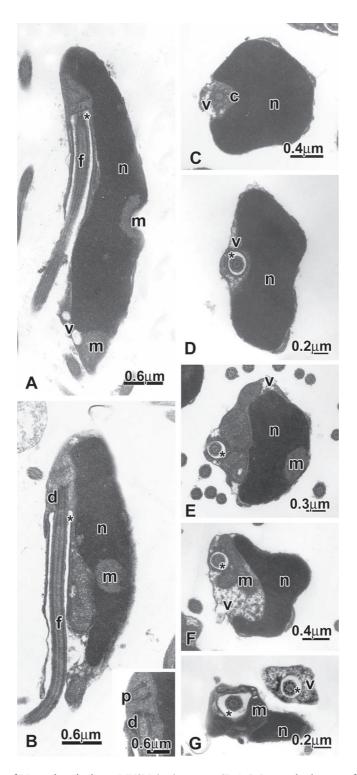


FIGURE 15: Spermatozoa of *Monotocheirodon kontos*, MUSM 6756, 38.1 mm SL. A, B: Longitudinal section of spermatozoa. Note lateral position of nucleus (n) relative to flagellar axis. Short midpiece containing mitochondria (m), several vesicles (v) and cytoplasmic canal (*) into which initial segment of flagellum fits (f). Proximal (p) and distal (d) centrioles located at very shallow nuclear fossa (B-inset) located near tip of nucleus. C-F: Cross section at different levels of nucleus showing strongly irregular nuclear outline, proximal centriole inside nuclear fossa (arrow), beginning of cytoplasmic canal (*) that houses initial segment of flagellum, elongate mitochondria between cytoplasmic canal and nuclear outline (E and F). Also note vesicles (v) visible along nuclear outline. G: Cross view at different levels of midpiece showing mitochondria accumulated especially at base of nucleus and decreasing progressively along midpiece. Cytoplasm of midpiece filled by vesicular system.

seen as electron dense dots (Fig. 15 J); the vesicles are intermingled with the mitochondria and are mainly external to them; this vesicular system and also the mitochondria are found in the midpiece at the base of the nucleus (Figs. 15, H-L). The midpiece, identical to that of *M. drilos* (Fig. 15 B) is about 0.7 μ m in length (SD \pm 0.1 μ m), and as in that species a single flagellum also emerges from the midpiece (Fig. 15 G).

Etymology: The name *kontos* is Greek masculine meaning a long pole. The word is used here in reference to the prominent male inseminating organ. A noun in apposition.

Distribution: Monotocheirodon kontos was collected in tributaries of the Río Madre de Dios basin, Peru (Fig. 7) between 350 and 3,200 m of altitude. It is sympatric with *M. drilos* in the Río Ebebahuaeji basin.

DISCUSSION

After its inclusion with inseminating clade A characids (Weitzman et al., 2005) and subsequently the subfamily Stevardiinae (Mirande, 2010; Oliveira et al., 2011) the first attempt to resolve the relationships of Monotocheirodon with the other stevardiin genera was by Ferreira et al. (2011). This involved 153 characters, including features of morphology, reproduction and sperm ultrastructure. Monotocheirodon kontos (the M. personi of those authors) was included as representative of the genus. Character analysis indicated that Monotocheirodon is closely related to and forms with the genus Otonocheirodus a separate clade within the Stevardiinae.

The two new species described herein share with *M. pearsoni* the presence of a single row of pedunculate, distally compressed multicuspid teeth on the premaxilla, the absence of an adipose fin, and the anal fin short with only 8-12 branched rays (characters 3, 8, and 9 of the diagnosis of the genus). These features are putatively considered non-exclusive synapomorphies that support the monophyletic condition of the genus. In the remaining stevardiines there are two rows of thick nearly rounded usually tricuspidate teeth, the adipose fin is usually present and the anal fin longer with more tham 12 rays.

Preliminary examination of *Ceratobranchia* cf. *delotaenia* (MZUSP 89678), *Bryconacidnus ellisi* (MUSM 11628), *Rhinopetitia* cf. *myersi* (MZUSP 36813), *Rhinopetitia* sp. (MZUSP 97176), *Otonocheirodus* sp. (MEPN 2787) and *Odontostoechus lethostigmus* (MCP 10774) cleared and stained for an ongoing

study of relationships, indicated that these genera share with *Monotocheirodon* at least characters 2, 6, and 7, described above in the diagnosis of that genus. These preliminary findings suggest that these five genera are more closely related among themselves than to any other stevardiin genus and probably represent a separate clade within the subfamily; however, a more comprehensive analysis of characters is required to confirm this hypothesis.

Oliveira *et al.* (2012) state that gill glands were found via histological preparations in mature inseminating males of *Monotocheirodon* species. No histological sections were conducted in this study to detect the presence of such structures.

The discovery that females of *Monotocheirodon drilos* and *M. kontos* also have a urogenital papilla, albeit smaller than that of the males, is intriguing. As demonstrated by Burns & Weitzman (2006) the male intromittent organs receive the sperm ducts from each testis and have a special circularly oriented skeletal muscle probably to avoid reflux of sperm during the process of its introduction into the oviduct. The function of the female urogenital papilla is unknown, but it might be used as a storage organ either for fertilized or unfertilized ovules prior to eggs release.

It is interesting that the absence of a male intromittent organ is correlated with the nearly spherical shape of the sperm nucleus in the externally fertilizing (aquasperm) of *Monotocheirodon pearsoni* whereas a small intromittent organ with ovoid sperm nuclei in *M. drilos* and a larger intromittent organ with more elongate nuclei in *M. kontos* occur in two internally fertilizing species. Other differences in sperm ultrastructure between the last two species as discussed above provide further evidence that they are different species.

RESUMO

Duas espécies novas de peixes inseminadores de água doce do Peru do gênero Monotocheirodon são descritas. Machos e fêmeas destas espécies têm uma papila urogenital bem visível externamente, não detectada nas fêmeas em estudos prévios, alongada e usada pelos machos como órgão inseminador. Uma terceira espécie inseminadora descrita da Bolívia, Monotocheirodon pearsoni, pouco estudada em detalhe desde sua descrição original em 1924, é redescrita. Esta última não possui órgão inseminador. O gênero Monotocheirodon é redescrito, suas relações filogenéticas com os demais gêneros incluídcos em Stevardiinae são brevemente discutidas, sugerindo-se que o mesmo possa estar relacionado com os gêneros Ceratobranchia, Otonocheirodus e Odontostoechus.

Seção de Publicações do MZUSP

Palavras-Chave: Peixes caracídeos inseminadores, novas espécies e relações de *Monotocheirodon*.

ACKNOWLEDGMENTS

The authors thank Tamara Clark for preparing Figs. 1, 2, 5, 6, 9, 10, 12, 13 and 14 with support from the Herbert R. and Evelyn Axelrod Chair in Systematic Ichthyology in the Division of Fishes, NMNH, which also provided funds for a trip of NAM to NMNH. The Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) supported research work of NAM in MZUSP and NMNH through a research fellowship. Lisa Palmer (NMNH) prepared radiographs and provided general curatorial assistance. Luiz Malabarba and Richard Vari supplied valuable input regarding discussions of inseminating characid fishes. Richard Vari provided assistance and working space to the senior author during his visit to USNM to study material of Monotocheirodon, read the manuscript, added useful suggestions and helped to improve the English version. Hernán Ortega (MUSM) and Jeffrey Clayton (NMNH) greatly contributed to this study by providing museum catalog numbers, loan of specimens, locality information and specimen data. Eduardo G. Baena (MZUSP) completed some drawings and provided computer assistance. José Birindelli, André Luiz Netto-Ferreira and Manoela Maria F. Marinho (MZUSP) helped with computer programs. Two anonymous reviewers provided valuable comments on the manuscript. We are gratefully indebted to all.

REFERENCES

- AYRES, M.; AYRES JR., M.; AYRES, D.L. & DOS SANTOS, A. DE A.S. 2007. BioEstat. Aplicações estatísticas nas áreas de ciências biomédicas. Belém, Pará, xvii + 359 p.
- BURNS, J.R. & WEITZMAN, S.H. 2006. Intromittent organ in the genus *Monotocheirodon* (Characiformes: Characidae). *Copeia*, 2006(3):529-534.
- Ferreira, K.M.; Menezes, N.A. & Quagio-Grassiotto, I. 2011. A new genus and two new species of Stevardiinae (Characiformes: Characidae) with a hypothesis on their relationships based on morphological and histological data. *Neotropical Ichthyology*, 9(2):281-298.
- FINK, W.L. & WEITZMAN, S.H. 1974. The so-called cheirodontin fishes of Central America with a description of two new species (Pisces: Characidae). Smithsonian Contributions to Zoology, 172:1-46.
- GÉRY, J. 1977. *Characoids of the World.* Neptune City NJ, T.F.H. Publications. 672 p.
- Lima, F.C.T.; Malabarba, L.R.; Buckup, P.A.; da Silva, J.F.P.; Vari, R.P.; Herald, A.; Benine, R.; Oyakawa, O.T.; Pavanelli, C.S.; Menezes, N.A.; Lucena, C.A.S.; Malabarba,

- M.C.S.L.; LUCENA, Z.M.S.; REIS, R.E.; LANGEANI, F.; CASATII, L.; BERTACO, V.A.; MOREIRA, C. & LUCINDA, P.H.F. 2003. Genera Incertae Sedis in Characidae. Pp. 106-169. *In:* Reis, R.E.; Kullander, S.O. & Ferraris, Jr., C.J. (Eds.). *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucrs. 729 p.
- MALABARBA, L.R. & WEITZMAN, S.H. 2000. A new genus and species of inseminating fish (Teleostei: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. *Proceedings of the Biological Society of Washington*, 1139(1):269-283.
- MALABARBA, L.R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). *In:* Malabarba, L.R.; Reis, R.E.; Vari, R.P.; Lucena, Z.M. & Lucena, C.A. (Eds.). *Phylogeny and Classification Neotropical Fishes.* Porto Alegre, Edipucrs. p. 193-233.
- MALABARBA, L.R. & WEITZMAN, S.H. 2003. Description of a new genus with six new species from Southern Brazil, Uruguay and Argentina, with a discussion of a putative characid clade (Teleostei: Characiformes: Characidae). Comunicações do Museu de Ciências e Tecnologia, PUCRS, Série Zoologia, 16(1):67-151.
- Menezes, N.A. & Weitzman, S.H. 1990. Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudin fishes of Brazil and Paraguay. *Proceedings of the Biological Society of Washington*, 103(2):380-426.
- Menezes, N.A. & Weitzman, S.H. 2009. Systematics of the neotropical fish subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*, 7(3):295-370.
- MIRANDE, J.M. 2010. Phylogeny of the famlily Characidae (Teleostei: Characiformes): from characters to taxonomy. Neotropical Ichthyology, 8(3):385-568.
- OLIVEIRA, C.; AVELINO, G.S.; ABE, K.T.; MARIGUELA, T.C.; BENINE, R.C.; ORTI, G.; VARI, R.P. & CASTRO, R.M.C. 2011. Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. *BMC Evolutionary Biology*, 11:1-25.
- OLIVEIRA, C.L.C. DE; MALABARBA, L.R. & BURNS, J.R. 2012. Comparative morphology of gill glands in externally fertilizing and inseminating species of cheirodontine fishes (Actinipterygii: Cheirodontinae), with implications on the phylogeny of the family Characidae. *Neotropical Ichthyology*, 10(12):349-360.
- PEARSON, N.E. 1924. The fishes of the eastern slope of the Andes, I: The fishes of the Rio Beni Basin, Bolivia, collected by the Mulford expedition. *Indiana Universities Studies*, 11(64):1-8.
- REYNOLDS, E.S. 1963. The use of lead citrate at high pH as an electron opaque stain in electron microscopy. *Journal of Cell Biology*, 17:208-212.
- Weitzman, S.H.; Menezes, N.A.; Evers, H-G. & Burns, J.R. 2005. Putative relationships among inseminating and externally fertilizing characids, with a description of new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae.). *Neotropical Ichthyology*, 3(3):329-360.

Aceito em: 27/03/2013 Impresso em: 30/06/2013

