

Astyanax laticeps (Teleostei: Characiformes: Characidae) from rivers and streams of Uruguay

MARÍA DE LAS MERCEDES AZPELIQUETA¹ & MARCELO LOUREIRO^{2,3}

¹ Conicet – Facultad de Ciencias Naturales y Museo, Paseo del Bosque, 1900 La Plata, Argentina
E-mail: azpeli(at)fcnym.unlp.edu.ar

² Sección Vertebrados, Departamento de Biología Animal. Facultad de Ciencias, Iguá 4225, Montevideo, Uruguay

³ Departamento de Ictiología. Museo Nacional de Historia Natural y Antropología. 25 de mayo 582
E-mail: mapy(at)fcien.edu.uy

Received on July 3, 2008, accepted on September 5, 2008.

Published online at www.vertebrate-zoology.de on May 15, 2009.

> Abstract

Astyanax laticeps (Teleostei: Characiformes: Characidae) from rivers and streams of Uruguay. – *Astyanax laticeps* is recorded from different streams of Laguna Merín, Laguna Castillos and Laguna de Rocha basins (Uruguay). The species is recognized by low body (28.2–37.3 % of SL), blunt snout, 1–4 maxillary teeth, 18–24 branched anal-fin rays, 36–39 perforated scales in lateral line, short caudal peduncle (12.6–13.7 % of SL), dorsal-fin origin nearer snout than caudal-fin rays origin, a horizontally oval or rounded humeral spot, surrounded by a light area, mature males with bony hooks on branched pelvic-fin rays and anteriormost anal-fins rays.

> Resumen

Astyanax laticeps (Teleostei: Characiformes: Characidae) en ríos y arroyos de Uruguay. – Se registra *Astyanax laticeps* en diferentes ríos y arroyos de las cuencas de la Laguna Merín, Laguna Castillos y Laguna de Rocha. La especie se distingue por el cuerpo bajo (28,2–37,3 % de LS), hocico romo, 1–4 dientes maxilares, 18–24 radios ramificados anales, 36–39 escamas perforadas en la línea lateral, pedúnculo caudal corto (12,6–13,7 % de LE), origen de aleta dorsal mas cerca del hocico que del origen de los radios caudales, una mancha humeral ovalada horizontalmente o redondeada, rodeada por una zona clara, machos maduros con ganchos óseos sobre los radios ramificados pélvicos y anales mas anteriores.

> Kurzfassung

Astyanax laticeps (Teleostei: Characiformes: Characidae) aus den Flüssen Uruguays. – *Astyanax laticeps* wird nachgewiesen in verschiedenen Wasserläufen der Laguna Merín, Laguna Castillos und Laguna de Rocha (Uruguay). Die Art ist erkennbar an ihrem niedrigen Körper (28,2–37,3 % SL), der stumpfen Schnauze; 1–4 Maxillarzähnen, 18–24 geteilten Analstrahlen, 36–39 durchbohrten Schuppen der Seitenlinie, einem kurzen Schwanzstiel (12,6–13,7 % SL), Beginn der Dorsale näher der Schnauze als dem Beginn der Caudalstrahlen, einem horizontalen ovalen oder runden Schulterfleck, der von einer hellen Zone umgeben ist, geschlechtsreife Männchen mit Hähchen auf den geteilten Bauchflossenstrahlen und den vordersten Flossenstrahlen der Analet.

> Key words

Laguna Merín, southern South America, *Astyanax*, geographical distribution.

Introduction

Several species of *Astyanax* – currently diagnosed as a combination of several broadly distributed features among Characidae – are known in the rivers of the República Oriental del Uruguay. MESSNER (1962) recorded several species and subspecies of *Astyanax* in rivers and streams of that country. Since that mo-

ment, no other articles are known concerning the genus *Astyanax* although several new species have been described in close regions (AZPELIQUETA & GARCÍA, 2000; BERTACO & MALABARBA, 2001; CASCIOTTA *et al.*, 2003). The examination of collections of Facultad de Ciencias (Universidad de la República, Uruguay) and Museo Nacional de Historia Natural y Antropología and those material studied by MESSNER (1962) allow us to record *Astyanax laticeps* (COPE, 1894) in streams

of Laguna Merín, Laguna Castillos, and Laguna de Rocha basins, giving measurements and description of this poorly known species.

Materials and Methods

Measurements are straight distances taken with calliper to nearest 0.1 mm. Standard length (SL) was measured from snout tip to border of hypurals; head length (HL) includes opercular flap; length of caudal peduncle is the distance between last anal-fin ray insertion and border of hypurals. Abbreviations for institutions from which material was examined include:

- AI**, Asociación Ictiológica, La Plata;
ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia;
CI-FML Fundación Miguel Lillo, Tucumán;
MACN Museo Argentino de Ciencias Naturales B. Rivadavia, Buenos Aires;
MLP Facultad de Ciencias Naturales y Museo, La Plata;
MNHN Museo Nacional de Historia Natural y Antropología, Montevideo;
MTD F Staatliches Museum für Tierkunde, Dresden;
URFGS Instituto de Biociências, Universidade Federal do Rio Grande do Sul;
ZVC-P Facultad de Ciencias, Universidad de la República, Montevideo.

Material. *Astyanax abramis* (JENYNS, 1842): MLP 9427, 2 ex., Argentina, Misiones, río Paraná. *Astyanax asuncionensis* GÉRY, 1972: MLP 8660, 5 ex., Argentina, Santiago del Estero, Bañado de Añatuya. MLP 8844, 7 ex., Argentina, Formosa, río Bermejo basin, arroyo Mbiguá. *Astyanax chico* CASCIOTTA & ALMIRÓN, 2004: MTD F 28331–28332, paratypes, Argentina, Salta, río San Francisco basin, arroyo Saladillo. *Astyanax correntinus* (HOLMBERG, 1891): MTD F 28 784, 2 ex., Argentina, Corrientes, río Paraná in Corrientes City. *Astyanax eigenmanniorum* (COPE 1894): ANSP 21627, paratypes, 2 ex., Brasil, Rio Grande do Sul; AI 180, 10 ex. (1 C&S), Brasil, Rio Grande do Sul, Viamão, açude Charolês and Arroio Viuva Tereza. *Astyanax endy* MIRANDE, AGUILERA & AZPELICUETA, 2004: CI-FML 3834, holotype, Argentina, Salta, Orán, río Bermejo basin, tributary of río Bermejo in its intersection with Ruta Provincial 19, near Estancia Santa Rosa. *Astyanax ita* ALMIRÓN, AZPELICUETA & CASCIOTTA, 2004: MLP 9599, holotype, Argentina, Misiones, río Iguazú basin, arroyo Tateto. *Astyanax laticeps*: AI 180, 1 ex. C&S, Uruguay, Rocha, arroyo Alférez, Laguna de Rocha basin. ANSP 21852, holotype, Rio Grande do Sul. MTD F 31585–31586, 2 ex., Uruguay, Rocha, arroyo Alférez, Laguna de Rocha basin. UFRGS 8976, 5 ex., Brazil, Rio Grande do Sul, São Sepé, Patos. UFRGS 8987, 5 ex., Brazil, Rio Grande do Sul, Herval Patos, unnamed stream (32° 00'S–53° 25'W). ZVC-P 1034, 22 ex., Uruguay, Cerro Largo, Road 8 and río Tacuarí, Merín-Patos basin. ZVC-P 3666, 9 ex., Uruguay, Treinta y Tres, Quebrada

de los Cuervos, arroyo Yermal chico, tributary of río Olimar, Merín-Patos basin. ZVC-P 1420, 2 ex., Uruguay, Lavalleja, arroyo Los Chanchos, tributary of río Cebollatí, Merín-Patos basin. ZVC-P 1765, 2 ex., Uruguay, Lavalleja, Villa Serrana, arroyo Los Chanchos, tributary of río Cebollatí, Merín-Patos basin. ZVC-P 3654, 2 ex., ZVC-P 3659, 2 ex., Uruguay, Treinta y Tres, Quebrada de los Cuervos, arroyo Yermal chico, tributary of río Olimar, Merín-Patos basin. ZVC-P 4788, 2 ex., Uruguay, Treinta y Tres, Quebrada de los Cuervos, arroyo Yermal chico, tributary of río Olimar, Merín-Patos basin. ZVC-P 5239, 3 ex., Uruguay, Cerro Largo, Paso del Duraznero, arroyo de la Mina, tributary of río Yaguarón, Merín-Patos basin. ZVC-P 5855, 2 ex. Rocha, A° Don Carlos, Laguna Castillos basin. ZVC-P 6192, 1 ex., Rocha, Paso Olivera, arroyo del Alférez, Laguna de Rocha basin. ZVC-P 6294, 3 ex., Uruguay, Rocha, stream in Sierra de Rocha, Laguna de Rocha basin. ZVC-P 6429, 3 ex., Uruguay, Cerro Largo, Paso del Duraznero, arroyo de la Mina, tributary of río Yaguarón, Merín-Patos basin. ZVC-P 7831, 1 ex., ZVC-P-7832, 1 ex., ZVC-P-7833, 10 ex., Uruguay, Treinta y Tres, Quebrada de los Cuervos, streams tributaries of A° Yermal chico, tributary of río Olimar, Merín-Patos basin. *Astyanax leonidas* AZPELICUETA, CASCIOTTA & ALMIRÓN, 2002: MLP 9580, holotype, Argentina, Misiones, río Paraná basin, headwaters of arroyo Urugua-í. *Astyanax ojiara* AZPELICUETA & GARCÍA, 2000: MLP 9470, holotype, Argentina, Misiones, arroyo Benítez. *Astyanax paris* AZPELICUETA, ALMIRÓN & CASCIOTTA, 2002: MLP 9584, Argentina, Misiones, arroyo Fortaleza, río Uruguay basin. *Astyanax rutilus* (JENYNS, 1842): MLP 7115, 1 ex., Argentina, Santa Fe, río Paraná basin. San José del Rincón. *Astyanax saguazu* CASCIOTTA, ALMIRÓN & AZPELICUETA, 2002: MLP 9603, holotype, Argentina, Misiones, río Uruguay basin, Arroyo Once Vueltas. *Astyanax cf. scabripinnis* (JENYNS, 1842): UFRGS 8191, 5 ex., Brazil, Rio Grande do Sul, Encruzilhada do Sul, Patos. UFRGS 8783, 4 ex., Brazil, Rio Grande do Sul, Pantano Grande, río Pardo, Patos. *Astyanax stenohalinus* MESSNER, 1962: MNHN 582, holotype, Uruguay, Departamento Cerro Largo, Laguna Mazangano, Río Negro basin. *Astyanax troya* AZPELICUETA, CASCIOTTA & ALMIRÓN, 2002: MACN 8310, holotype, Argentina, Misiones, Arroyo Cuñapirú Chico. *Astyanax tupi* AZPELICUETA, MIRANDE, ALMIRÓN & CASCIOTTA, 2003: MACN-Ict 8646, holotype, Argentina, Misiones, Arroyo Cuñapirú Chico.

Astyanax laticeps (COPE, 1894)

Figs. 1–3, table 1

Description. Morphometrics of 18 specimens are presented in Table 1. Body low (2.67–3.54 times in SL), scarcely deeper at vertical through posterior third of pectoral fin. Dorsal profile of body slightly convex from snout tip to point of maximum depth, very gently convex to dorsal-fin origin (Fig. 1, 2); slightly slanted ventrally from this point to caudal peduncle. Dorsal and ventral profiles of caudal peduncle straight. Ventral profile of body convex from lower jaw tip to pelvic-fin origin; straight between pelvic and anal fin, slanted dorsally to caudal peduncle.



Fig. 1. *Astyanax laticeps*, ZVCP 6192, Uruguay, Departamento de Rocha, Arroyo Alferez, Rincón del Alferez, Laguna de Rocha basin (Uruguay).



Fig. 2. *Astyanax laticeps*, UFRGS 8987, Brazil, Rio Grande do Sul, Herval, laguna dos Patos system (32°00'48''S–053°25'37''W).



Fig. 3. *Astyanax laticeps*, a fresh specimen from arroyo Alferez, in Rincón del Alferez, Dep. Rocha, ZVCP 5855.

Dorsal-fin origin located nearer snout tip than base of caudal-fin rays. Pelvic-fin origin located anterior to vertical through dorsal-fin origin. Anal-fin origin located notably behind vertical line through base of last

Tab. 1. Measurements of 18 specimens of *Astyanax laticeps* from streams of Uruguay. Body depth 1 indicates body depth at dorsal-fin origin; body depth 2 indicates depth at vertical through middle pectoral-fin.

| SL | min | max | mean | SD |
|--|------|------|------|--------|
| % of standard length | | | | |
| predorsal length | 41.6 | 55.9 | 51.6 | 2.2467 |
| prepelvic length | 45.3 | 50.7 | 48.4 | 1.4166 |
| preanal length | 63.2 | 69.1 | 66.2 | 1.5516 |
| body depth 1 | 28.2 | 37.3 | 33 | 2.3225 |
| body depth 2 | 28 | 33.8 | 30.5 | 1.59 |
| dorsal-fin base | 11.8 | 17.8 | 13.9 | 1.2378 |
| anal-fin base | 23.3 | 33.1 | 26.3 | 2.1184 |
| pectoral-fin length | 19 | 24.1 | 21 | 1.4224 |
| pelvic-fin length | 14.8 | 20.3 | 17.2 | 1.4536 |
| length between pectoral and pelvic fin origins | 20.7 | 25.4 | 23 | 1.2397 |
| length between pelvic and anal fin origins | 15.6 | 21.8 | 19.2 | 1.4951 |
| peduncle depth | 11.3 | 14.8 | 12.3 | 0.9261 |
| peduncle length | 13.1 | 18 | 15.2 | 1.4584 |
| head | 28.3 | 35.7 | 29.7 | 1.7684 |
| % of head length | | | | |
| eye | 24 | 31.7 | 28.5 | 2.1509 |
| snout | 20.8 | 26 | 23.4 | 1.7041 |
| postorbital | 45.2 | 57.1 | 53.6 | 2.8792 |
| interorbital | 24 | 37.2 | 33.8 | 3.2021 |
| upper jaw length | 34.8 | 43.6 | 40.2 | 2.4839 |

dorsal-fin rays in most specimens. Tip of pectoral fin far from pelvic-fin origin even in small specimen. Tip of pelvic fin reaching anal-fin origin in small although far from it in adults.

Dorsal fin with iii, 9, first branched dorsal fin rays longest. Anal fin with iv–v, 18(3 ex.), 19(9 ex.), 20(2 ex.), 21(3 ex.), 24 (1 ex.) rays; anterior lobe small, slightly rounded. Males with hooks on 7–11 branched anal-fin rays, only on posterior branch of rays, one pair of broad hooks per segment. Caudal fin with principal rays i, 17, i. Pectoral fin with i, 10(3 ex.), 11(7 ex.), 12(5 ex.), 13 (2 ex.), 14 (1 ex.) rays. Pelvic fin with i, 7 rays; males bearing hooks on 1 to 5 branched rays, only on posterior branch, one pair of broad hooks per segment.

Mouth terminal, located at level of inferior third of eye or less. Premaxilla bearing two series of teeth. Outer row with 2 (3 ex.), 3 (2 ex.), 4 (14 ex.), or 5 (1) tricuspidate teeth, with base slightly broader than tip; inner row with 5 teeth (1 specimens with 6) slightly concave anteriorly; symphyseal tooth slender with 4 cusps, second tooth with 6–7 cusps, third and fourth teeth with 5–7 cusps, fifth teeth small tricuspidate. Ascending process of maxilla very slender; laminar process of maxilla surpassing anterior margin of eye bearing 1 (1 ex.), 2 (11 ex.), 3 (4), 4 (2 ex.) tri to unicuspidate teeth. Dentary with anterior 3 pentacuspidate teeth, one medium sized pentacuspidate, followed by 5–6 very small teeth tri to unicuspidate, all of them with very broad bases.

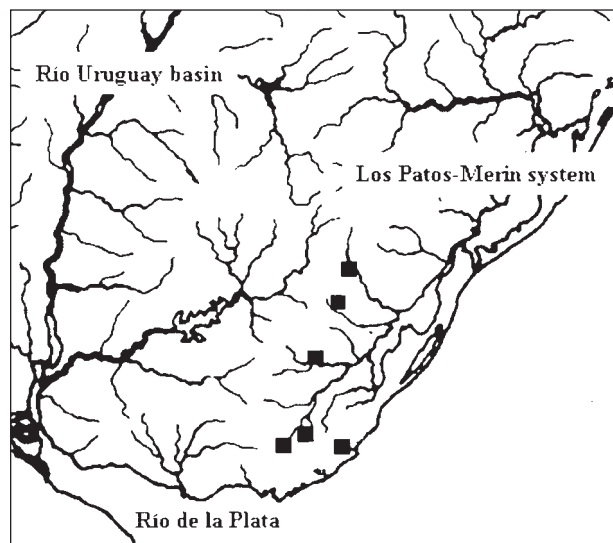


Fig. 4. Geographical distribution of *Astyanax laticeps* in Uruguay. Localities belong to laguna Merín, laguna Castillos, and laguna de Rocha basins.

Scales cycloid, without circuli on posterior field. Lateral line with 36 (4 ex.), 37 (8 ex.), 38 (5 ex.) or 39 (1) perforated scales. Scales between dorsal-fin origin and lateral line 6–7; scales between lateral line and pelvic fin origin 5–6. Scales around caudal peduncle 17 (2) or 18 (16). Scales between tip of supraoccipital spine and base of dorsal fin 12–14, usually forming an irregular row. Short row of scales forming a sheath covering base of unbranched and first 10 branched



Fig. 4. Different environments where *A. laticeps* was collected. Uruguay, Departamento Treinta y Tres, quebrada de los Cuervos. A. arroyo Yermal Chico; B. hedwater pond of a tributary of arroyo Yermal Chico; C. high slope isolated pool, tributary of arroyo Yermal Chico.

anal-fin rays. Few scales covering only the base of caudal-fin lobes.

First branchial arch with 17–19 gill rakers: 6–7 on epibranchial, 1 on cartilage, 10–11 on ceratobranchial (ten specimens).

Colour of alcohol preserved specimens. Flanks of body darker dorsally; head dark; chromatophores located on posterior margin of scales forming a reticu-

lar pattern especially notable on upper half of flanks, although present on anteroventral region of body in most specimens. In some specimens, there are concentrations of chromatophores between scales forming lines that resembles those of *A. lineatus*. One black humeral spot horizontally oval or rounded, surrounded by a light area. A vertically elongated projection of this humeral spot in few specimens. Origin of black wide lateral stripe at different levels but usually close

to humeral spot, lateral stripe ending at tip of caudal-fin rays with a broader area on caudal peduncle. Tip of dorsal fin dusky; margin of caudal fin darker; paired fins hyaline. A fresh specimen from arroyo Alférez is shown in figure 3.

Distribution and biological notes. All localities where *A. laticeps* were found are over 50 meters above sea level, in tributaries of the main rivers of Laguna Merin basin, and tributaries of Laguna Castillos and Laguna de Rocha basins. Furthermore, recent collections in the protected area of Quebrada de los Cuervos (tributaries of río Olimar, Dep. Treinta y Tres, Fig. 4A) include juvenil and adult specimens from small upstream isolated ponds and pools, temporary disconnected from main creeks and streams. The juveniles were found in ponds located in the head waters of streams (Figure 4B) while adults were found in those places and also in isolated pools of high slope streams (descending 60 meters in less than 500 meters) (Figure 4C).

Discussion

EIGENMANN (1921, 1927) included several subspecies of *Astyanax scabripinnis* in his large paper about Characidae, being one of them *A. s. laticeps*. MALABARBA (1989) restricted the geographical distribution of *A. s. laticeps* to the Laguna dos Patos system, in Brazil. BERTACO & MALABARBA (2001) demonstrated that some of the subspecies of the *A. scabripinnis* complex are valid species. LIMA *et al.* (2003) mentioned *A. laticeps* also considering its distribution restricted to Rio Grande do Sul, in the laguna dos Patos system although with a question mark.

MESSNER (1962) studied some samples included in this paper, identifying them as *A. scabripinnis* (ZVC P 1427), *A. s. paranae* (ZVC P 1428, ZVC P 1420), and *A. s. laticeps* (ZVC P 1765). All those specimens correspond to *A. laticeps*. *Astyanax laticeps* is distinguished from other species of *Astyanax* by low body, scarcely deeper at dorsal-fin origin (28.2–37.3 % of SL at dorsal-fin origin, 28.0–33.8 taken at the level of a vertical through middle pectoral fin); blunt snout; 1–4 maxillary teeth; 18–24 branched anal-fin rays; 36–39 perforated scales in lateral line; 6–7/5–6 transverse scales; short caudal peduncle (12.6–13.7 % of SL); dorsal-fin origin nearer snout than caudal-fin rays origin; a horizontally oval or rounded humeral spot, surrounded by a light area; bony hooks of males restricted to 1–5 branched pelvic rays and 7–11 anterior-most anal-fins rays of mature males.

Astyanax laticeps is found in different rivers and streams of the laguna Merín, laguna Castillos, and la-

guna de Rocha basin, in Uruguay (Fig. 4). Although, the later lagoons basins currently outflow to the Atlantic Ocean, the distribution of this species support a past connection of these systems to those of Laguna Merín. This scenario may correspond to the sea level fluctuations reported for this region (SPRECHMANN, 1978; MONTAÑA & BOSSI, 1995; GARCÍA-RODRIGUEZ, 2003) or basin capture events that connected these water bodies. Moreover, at least other seven endemic species of the laguna dos Patos-Merín system are present in Laguna Castillos tributaries (*Mimagoniates inequalis*, *Heptapterus sympterigium*, *Hyphessobrycon boulengeri*, *Austrolebias cheradophilus*, *A. viarius*, *A. luteoflamulatus*, and *Cynopoecilus melanotaenia*) and other one in Laguna de Rocha tributaries (*Austrolebias luteoflamulatus*) (LOUREIRO & GARCÍA, 2006). Comparisons with specimens from Brazil (see material and Fig. 2) reveal same characters and measurements.

Acknowledgments

Authors thank John Lundberg and Mark Sabaj (ANSP) and Luiz Malabarba (UFRGS) for loan of specimens, Vinicius Bertaco (MCP) for information about the holotype of *Astyanax laticeps*, G. García (FC) and Matías Zarucki (FC) for collection of specimens, Conicet for permanent financial support to MMA, CSIC and SNAP for financial support to ML.

References

- AZPELICUETA, M. DE LAS M. & GARCÍA, J.O. (2000): A new species of *Astyanax* (Characiformes, Characidae) from Uruguay river basin in Argentina, with remarks on hook presence in Characidae. – *Revue suisse de Zoologie*, **107**(2): 245–257.
- BERTACO, V.A. & MALABARBA, L.R. (2001): Description of two new species of *Astyanax* (Teleostei: Characidae) from headwater streams of Southern Brazil, with comments on the “*A. scabripinnis* species complex”. – *Ichthyological Exploration of Freshwaters*, **12**(3): 221–234.
- CASCIOTTA, J.R., ALMIRÓN, A.E. & AZPELICUETA, M. DE LAS M. (2003): A new species of *Astyanax* from río Uruguay basin, Argentina (Characiformes, Characidae). – *Ichthyological Exploration of Freshwaters*, **14**(4): 329–334.
- EIGENMANN, C.H. (1921): The American Characidae. – *Memoirs of the Carnegie Museum* **23**(2): 209–310.
- EIGENMANN, C.H. (1927): The American Characidae. – *Memoirs of the Carnegie Museum*, **23**(3): 311–428.
- GARCÍA-RODRÍGUEZ, F. & WITKOWSKI, A. (2003): Inferring sea level variation from relative percentages of *Pseudopodosira kosugii* in Rocha Lagoon, SE Uruguay. – *Diatom Research* **18**(1): 49–59.

- LIMA, F.C.T., MALABARBA, L.R., BUCKUP, P.A., PEZZI DA SILVA, J.F., VARI, R.P., HAROLD, A., BEBINE, R., OYAKAWA, O.T., PAVANELLI, C.S., MENEZES, N.A., LUCENA, C.A.S., MALABARBA, M.C.S., LUCENA, Z.M.S., REIS, R.E., LANGEANI, F., CASSATI, L., BERTACO, V.A., MOREIRA, C. & LUCINDA, P.H.F. (2003): Genera Incertae Sedis in Characidae: 106-169, in: REIS, R.E., KULLANDER, S.O. & FERRARIS, C.J.Jr (eds.): Checklist of the Freshwaters fishes of South and Central America. EDIPUCRS, Porto Alegre, Brazil.
- LOUREIRO, M. & GARCÍA, G. (2006): Transgresiones y regresiones marinas en la costa atlántica y lagunas costeras de Uruguay: efectos sobre los peces continentales. En "Bases para la Conservación y el manejo de la costa uruguaya", (R. Menafrá, L. Rodríguez-Gallego, F. Scarrabino, D. Conde eds.). Vida Silvestre-Uruguay.
- MALABARBA, L.R. (1989): Histórico sistemático e lista comentada das espécies de peixes de água doce do sistema da Laguna dos Patos, Rio Grande do Sul, Brasil. – Comunicações do Museu de Ciências, PUCRS, Série Zoologia, **2**(8): 107–179.
- MESSNER, E. (1962): Lista de los peces tetragonopterinae (familia Characidae) del Uruguay. – Boletín de la Asociación Latinoamericana de Ictiólogos y Herpetólogos, **2**: 1–4.
- MONTAÑA, J.R. & BOSSI, J. (1995): Geomorfología de los humedales de la cuenca de la Laguna Merín en el departamento de Rocha. – UDELAR. Fac. de Agronomía. Montevideo. Serie 2: 1–32.
- SPRECHMAN, P. (1978): The paleoecology and paleogeography and stratigraphy of the uruguayan coastal area during the neogene and quaternary. – Zitteliana, **4**: 3–72.