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Colouration, taxonomy and geographical distribution of mangrove killifishes, the *Kryptolebias marmoratus* species group, in southern Atlantic coastal plains of Brazil (Cyprinodontiformes: Rivulidae)

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New data on colouration, taxonomy and distribution of the three species of mangrove killifishes, the *Kryptolebias hermaphroditus* group, in the southern hemisphere are provided, including the first description of male colouration in *K. hermaphroditus*. Two characters of the male colour pattern of *K. hermaphroditus* are useful to distinguish it from its closest congener, *K. marmoratus*, including the presence of a broad black margin along the whole caudal fin, bordered by a broad sub-marginal white zone, and absence of bright orange pigmentation on the head and trunk. There are two distinct colour morphs in males of both *K. hermaphroditus* and *K. ocellatus*, a condition not occurring in other Neotropical aplocheiloids, but reported in African aplocheiloids. *Kryptolebias marmoratus* occurs in northeastern Brazil but its southern-most record is separated by about 1100 km from the distribution area of *K. hermaphroditus* that is endemic of south-eastern Brazilian coastal plains. *Kryptolebias marmoratus* is found in euryhialine mangrove habitats, often under direct influence of sea water, whereas *K. hermaphroditus* is found in brackish and freshwater coastal streams and channels. The distribution area occupied by *K. ocellatus* in southern and south-eastern Brazil overlaps the area occupied by *K. hermaphroditus* in localities within the Guanabara and Sepetiba bays.

Introduction

Species of the *Kryptolebias marmoratus* group have been popularly called mangrove killifishes. The best known mangrove killifish is *K. marmoratus* (Poey, 1880), a small species reaching a total length of about 70 mm, with peculiar biology, including self-fertilizing hermaphroditism and ability to survive in estuarine habitats with extreme environmental conditions (Harrington, 1961; Abel et al., 1987; King et al., 1989; Davis et al., 1990; Dunson & Dunson, 1999). For example, besides living both in saltwater and neighbouring freshwater parts of mangroves, it is often found out of water, exhibiting complex strategies for aerial respiration (Wright, 2012; Turko et al., 2014). This uncommon combination of biological characteristics makes *K. marmoratus* among the most popular experimental fish species, with numerous publications in disciplines ranging from behaviour to carcinogenesis (e. g., Lee et al., 2008; Earley et al., 2012).

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Fig. 1. *Kryptolebias hermaphroditus*, UFRJ 10405; Brazil: Espírito Santo: Coqueiral. **a,** dark morph male, 45.9 mm SL; **b,** light morph male, 45.0 mm SL; **c,** hermaphrodite, 41.3 mm SL.

Kryptolebias marmoratus is geographically widespread along estuarine zones of southern North America, Bahamas, Antilles, western Central America, and northern South America. The *K. marmoratus* group also includes *K. hermaphroditus* Costa, 2011 and *K. ocellatus* (Hensel, 1868) from south-eastern and southern Brazil (Costa, 2011), all the three being androdoecius species (i.e., natural populations consisting of males and hermaphrodites, never females), a rare condition among vertebrates, whereas *K. marmoratus* and *K. hermaphroditus* are the only self-fertilizing hermaphrodites among vertebrates (Harrington, 1961; Costa et al., 2010).

In spite of the increasing popularity of *K. marmoratus* as an experimental fish, the taxonomy of the *K. marmoratus* species group has been confused. Before 2004, all species presently included in *Kryptolebias* Costa, 2004 were placed in *Rivulus* Poey, 1860, then a paraphyletic assemblage comprising numerous unrelated species (Hrbek & Larson, 1999; Murphy et al., 1999). Costa (2004) provided substantial morphological evidence supporting *Kryptolebias* as a distinct genus, constituting the sister group of all other rivulids.

More problematic than the generic position of *Kryptolebias* has been the taxonomy of species of the *K. marmoratus* group. The taxonomical problems started with Garman's (1895) review of cyprinodontiforms, who equivocally placed *Rivulus marmoratus* in the synonymy of *R. cylindraceus* Poey, 1860. This synonymy resulted in 50 years of misidentifications until the type specimen revision conducted by Rivas (1945) clarified the status of both species. Among southern Atlantic species, just recently Costa (2011) based on examination of type specimens demonstrated that the species known between 1984 and 2011 as *K. caudomarginatus* (Seegers, 1984) is a synonym of *K. ocellatus*, and that the species identified as *K. ocellatus* in that same period was in fact a new species, then described as *K. hermaphroditus*.

Our present knowledge on geographical distribution of mangrove killifishes in the southern Atlantic coastal plains is still incomplete (Tatarenkov et al., 2015), mostly restricted to Rio de Janeiro and

Fig. 2. Geographical distribution of species of mangrove killifishes, the *Kryptolebias marmoratus* group, in southern Atlantic coastal plains, Brazil.

São Paulo states, in south-eastern Brazil (Costa, 2006, 2011). In addition, colour pattern of males, which usually constitute an important tool for species recognition and diagnosis of aplocheiloid killifishes, have been poorly documented for southern Atlantic populations of mangrove killifishes. In *K. hermaphroditus*, colouration of males is still completely unknown since no male was recorded among the 70 preserved specimens used in its recent description, the species being known only from hermaphroditic specimens (Costa, 2011).

Between 2013 and 2014, during collections directed to estuarine zones of southern and south-eastern Brazil, males of *K. hermaphroditus* were found at two localities. The first description of male specimens of *K. hermaphroditus* is herein provided, as well as a revision of available data about colour pattern variability and geographical distribution in the *K. marmoratus* group in the southern Atlantic coastal plains.

Material and methods

Descriptions of colour patterns were based on direct examination of live specimens in aquaria just after collection, and photographs of both sides of live individuals taken between one and three days after collections. Abbreviations for institutions cited in the text are: AMNH, American Museum of Natural History, New York; IZAC, Instituto de Zoología, Academia de Ciencias de Cuba, La Habana; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MNHN, Muséum National d'Histoire Naturelle, Paris; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; UFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; USNM, National Museum of Natural History (former United States National Museum), Smithsonian

Institution, Washington; ZFMK, Zoologisches Forschungsmuseum und Museum Alexander Koenig, Bonn; ZMA, Instituut voor Systematiek and Populatiebiologie, Amsterdam; and, ZMB, Museum für Naturkunde, Berlin.

Kryptolebias hermaphroditus Costa, 2011
(Fig. 1)

Kryptolebias hermaphroditus Costa, 2011: 187 (holotype: UFRJ 6863; type-locality: canal near EMBRAPA, Piracão river basin, a tributary of the Sepetiba bay, Guaratiba, Município do Rio de Janeiro, Estado do Rio de Janeiro, Brazil, 23°00'18"S 43°33'35"W).

Material examined. BRAZIL: ESTADO DO RIO DE JANEIRO: UFRJ 6863, holotype; UFRJ 6243, 2 paratypes; canal near EMBRAPA, Piracão river basin, a tributary to Sepetiba bay, Guaratiba, Município do Rio de Janeiro, 23°00'18"S 43°33'35"W; W. J. E. M. Costa et al., 14 Aug 2005. – UFRJ 6234, 4 paratypes; same locality; W. J. E. M. Costa et al., 2004. – UFRJ 6237, 3 paratypes; same locality; W. J. E. M. Costa et al., 19 Feb 2005. – UFRJ6252, 9 paratypes; same locality; W. J. E. M. Costa et al., 22 Oct 2005. – MNRJ 25388, 1 paratype; same locality; J. R. Gomes, 12 Feb 2003. – MNRJ 25384, 2 paratypes; same locality; J. R. Gomes, 5 Feb 2003. – MNRJ 26427, 4 paratypes; same locality; J. R. Gomes, 22 Oct 2003. – MNRJ 25513, 8; same locality; J. R. Gomes, 15 May 2003. – MNRJ 26444, 2 paratypes; swamp near southern margin of Marapendi lagoon, 4 km from Pedra do Pontal, Município do Rio de Janeiro, 23°01'08"S 43°26'02"W; J. R. Gomes, 13 May 2003. – MNRJ 2504, 5 paratypes; near southern margin of Marapendi lagoon, 200 m from Recreio beach, about 7 km from Pedra do Pontal, Município do Rio de Janeiro, 23°00'52"S 43°24'20"W; J. R. Gomes, 21 Dec 2002. – MNRJ 25363, 8 paratypes; swamp about 5 km from Pedra do Pontal, Município do Rio de Janeiro, 23°01'02"S 43°25'28"W; J. R. Gomes, 28 Dec 2002. – UFRJ 1806, 3; swamp near Itaguaí, Sepetiba bay, Município de Itaguaí, 22°54'01"S 43°49'31"W; M. S. Melgaço, 25 Jul 1991. – MNRJ 25351, 4; small canal near Portinho River, das Américas Avenue, Município do Rio de Janeiro, 23°00'25"S 43°33'06"W; J. R. Gomes, 5 Jan 2003. – MZUSP 38369, 1; MZUSP 38441, 1; brackish-water channel near Araruama lagoon, Iguaba Grande, 22°50'31"S 42°12' 26"W; W. J. E. M. Costa et al., Jan 1983. – MZUSP 38335, 5; Mangaratiba, 22°57'54"S 44°02'36"W; M. T. C. Lacerda & J. C. Ghisolfi, 1986. – MNRJ 19483, 5; MNRJ 19548, 3; road Amaral Peixoto, km 150-152, Município de São Pedro da Aldeia, 22°49'43"S 42°07'35"W; C. A. G. Cruz et al., 19 Aug 1973. – MNRJ 19549, 1; Modelo Farm, Sepetiba bay, Município do Rio de Janeiro, 22°59'40"S 43°35'34"W; C. A. G. Cruz, 18 Sep 1971. – UFRJ 10406, 1; mangrove channel in Divinéia village, Fundão island, Guanabara bay, Município do Rio de Janeiro, 22°52'11"S 43°13'03"W; G. Silva, 27–28 Feb 2013. – UFRJ 10294, 4; mangrove near Divinéia village, Fundão island, Guanabara bay, Município do Rio de Janeiro, 22°52'03"S 43°13'21"W; J. L. O. Mattos et al., 2 Dec 2014. – UFRJ 10063, 2; mangrove channel draining into Araruama lagoon, 22°55'07"S 42°21'59"W, Município de Araruama; P. F. Amorim & F. Rangel, 17 Jul 2014. – UFRJ 10064, 1; channel draining into Araruama lagoon, Seca beach, 22°53'39"S 42°23'12"W, Município de Araruama; P. F. Amorim & F. Rangel, 17 Jul 2014. ESTADO DO ESPÍRITO SANTO: UFRJ 10405, 14; UFRJ 10278, 6; stream in Coqueiral beach, Município de Aracruz, 19°56'05"S 40°07' 49"W; W. J. E. M. Costa et al., 1 Dec 2014. ESTADO DE SÃO PAULO: UFRJ 6300, 5; UFRJ 6301, 2; mangrove near Picinguaba, 23°22'11"S 44°50'12"W; L. Villa-Verde et al., 19 Nov 2005.

Colouration. Males. Dark morph: flank dark brownish purple, with vertical rows of bluish silver spots. Dorsum greenish brown, venter white; nearly rounded, black blotch on humeral region. Head side and jaws dark brownish purple, with bluish silver iridescence on opercle. Iris brown. Dorsal and anal fins grey, with narrow black distal margin and bluish white sub-marginal stripe; dark grey to black dots on basal portion of dorsal fin, sometimes pale grey dots on basal portion of anal fin. Caudal fin orangish grey on basal portion and yellowish white on middle portion, with broad black margin. Pectoral fin hyaline, pelvic fin white. Light morph: flank bluish silver, with dark red spots irregularly arranged, often forming oblique and horizontal rows of coalesced spots; inconspicuous grey humeral spot, more visible in preserved specimens. Dorsum greenish brown, venter white. Head side and jaws purplish silver, with golden iridescence on opercle, and brown blotches on post-orbital region. Iris brown. Dorsal and anal fins pale grey, with narrow black distal margin and white sub-marginal stripe; dark grey dots on basal portion of dorsal fin. Caudal fin orangish grey on basal portion and yellowish white on middle portion, with broad black margin. Pectoral fin hyaline, pelvic fin white.

Hermaphrodites. Flank dark purplish or brownish grey, with horizontal rows of pale silver or pale golden spots on dorsal portion of flank; nearly rounded, black blotch on humeral region. Round black spot with yellowish white margin on postero-dorsal portion of caudal peduncle. Dorsum greenish brown, venter white. Head side and jaws brownish grey, with pale golden iridescence on opercle. Iris brown. Unpaired fins hyaline, with transverse series of dark grey dots on basal region; distal margin of anal fin and

ventral margin of caudal fin often with narrow light grey stripe. Paired fins hyaline.

Geographical distribution and habitat. *Kryptolebias hermaphroditus* is endemic to the south-eastern Brazilian coast (Fig. 2). It is here confirmed for the area between Coqueiral beach, in Espírito Santo state (19°56'05"S 40°07'49"W) and Picinguaba mangrove, in São Paulo state (23°22'11"S 44°50'12"W). It is sympatric with *K. ocellatus* in the Guanabara bay and Sepetiba bay mangroves. *Kryptolebias hermaphroditus* is usually found in brackish water of estuarine areas, mostly associated to mangroves, in channels and stream banks, often close to the grass concentrated on stream bank. Sometimes it inhabits freshwater parts of coastal streams within coastal forests, a few meters above the estuarine zone.

Male occurrence and colour pattern frequency. Among eight populations here studied, males were present only in two localities, Coqueiral beach (19°56'05"S 40°07'49"W) and Divinéia mangrove (22°52'03"S 43°13'21"W). In Coqueiral beach, three males were found among 20 specimens collected, one with the light morph pattern and two with the dark morph as described above. All the remaining 17 specimens were hermaphrodites exhibiting the typical hermaphrodite colour pattern described above and in Costa (2006, 2011). In Divinéia mangrove, we found two males, both belonging to the light morph, and 18 hermaphrodites.

Kryptolebias ocellatus (Hensel, 1868)
(Fig. 3)

Rivulus ocellatus Hensel, 1868: 365 (holotype: ZMB 7448; type-locality: Rio de Janeiro [presently Município do Rio de Janeiro, Estado do Rio de Janeiro, Brazil].

Rivulus caudomarginatus Seegers, 1984: 307 (holotype: ZFMK 12848; type locality: Greta Funda [correctly Grota Funda, an equivocal locality as discussed by Costa, 2006], near a technical centre of the Army, southern Rio de Janeiro, Brazil [corrected by Costa, 2006 to: near Technological Centre of the Brazilian Army, Guaratiba, south-western Município do Rio de Janeiro, south-eastern Brazil, Rio Piracão basin, a tributary to Baía de Sepetiba, 23°00'18"S 43°33'35"W]).

Material examined. BRAZIL. ESTADO DO RIO DE JANEIRO: ZMB 7448, holotype of *R. ocellatus*; Rio de Janeiro; no data on collection. – ZFMK 12848, holotype of *R. caudomarginatus*; near Centre of Brazilian Army, Guaratiba, Rio de Janeiro (23°00'18"S 43°33'35"W according to Costa, 2006). – UFRJ 9294, 5; mangrove channel near Vila da Divinéia, Fundão island, Município do Rio de Janeiro, 22°52'11"S 43°13'03"W; G. Silva, 27–28 Feb 2013. – UFRJ 10293, 8; Município do Rio de Janeiro: mangrove near Vila da Divinéia, Fundão island, Município do Rio de Janeiro, 22°52'03"S 43°13'21"W; J. L. O. Mattos et al., 2 Dec 2014. – UFRJ 6235, 15; UFRJ 6236, 6; canal near EMBRAPA, Piracão river basin, a tributary to Sepetiba bay, Guaratiba, Município do Rio de Janeiro, 23°00'18"S 43°33'35"W, altitude 8 m asl; W. J. E. M. Costa et al., 2004. – UFRJ 6238, 4; same locality; W. J. E. M. Costa et al., 19 Feb 2005. – UFRJ 6244, 12; same locality; W. J. E. M. Costa et al., 14 Aug 2005. – UFRJ 6253, 4; same locality; W. J. E. M. Costa et al., 22 Oct 2005. – UFRJ 10409, 23; same locality; W. J. E. M. Costa et al., 30 Apr 2009. – UFRJ 4816, 30; flooded mangrove area near Barão de Iriri, Município de Magé 22°40'28"S 43°03'40"W; W. J. E. M. Costa et al., 4 Dec 1998. – UFRJ 6520, 7; 7; Município de Itaguaí, 22°54'00"S 43°46'47"W; F. Leal, Feb 2008. – UFRJ 1047, 14; UFRJ 5583, 3; Madeira mangrove, Município de Itaguaí, 22°54'01"S 43°49' 31"W; M. S. Melgaço, 13 Nov 1991. – UFRJ 1805, 32; same locality; M. S. Melgaço, 25 Jul 1991. ESTADO DE SÃO PAULO: UFRJ 2084, 9; UFRJ 5584, 2; flooded area near sea channel separating Cananéia island and continent, 24°59'05"S 47°57'08"W; W. J. E. M. Costa & C. P. Bove, 30 Dec 1993. ESTADO DE SANTA CATARINA: UFRJ 6342, 36; UFRJ 6343, 5; UFRJ 6344, 4; mangrove close to Linguado channel, in small island close to bridge between São Francisco island and continent, 26°21'55"S 48°39'54"W; W. J. E. M. Costa et al., 19 Dec 2005. – UFRJ 10394, 7; UFRJ 10246, 11; same locality; W. J. E. M. Costa et al., 26 Sep 2014. – UFRJ 10529, 14; UFRJ 10636, 4 (c&s); lagoon near Tubarão river mouth, Município de Laguna, 28°31'16"S 48°50'47"W; C. Feltrin, 5 Jun 2015. – UFRJ 10530, 40; UFRJ 10531, 4; UFRJ 10483, 6; same locality; C. Feltrin et al., 10 Jun 2015.

Colouration. Males. Dark morph: flank bluish silver, with dark grey to black bars and spots; rounded black blotch on humeral region. Dorsum greenish brown, venter white. Head side and jaws purplish grey. Iris brown. Dorsal and anal fins pale grey, with black spots on basal half of fin, and with black distal margin and bluish white sub-marginal band. Caudal fin dark grey, with broad black margin and broad sub-marginal white zone; round black spot on dorso-basal portion of caudal fin. Pectoral fin hyaline, pelvic fin white.

Light morph. Flank bluish silver, with dark grey spots, sometimes reddish grey, irregularly arranged, often forming oblique rows of coalesced

Fig. 3. *Kryptolebias ocellatus*, UFRJ 10394; Brazil: Santa Catarina: Linguado channel. **a,** dark morph male, 35.5 mm SL; **b,** light morph male, 38.2 mm SL; **c,** hermaphrodite, 37.2 mm SL.

spots; rounded black blotch on humeral region. Dorsum greenish brown, venter white. Head side and jaws purplish grey. Iris brown. Dorsal and anal fins pale grey, with grey or black spots on basal half of fin, and with light or dark grey distal margin and white or orangish white sub-marginal band. Caudal fin orangish grey, with dark grey margin, darker and broader on ventral portion, and broad sub-marginal orangish white zone; round black spot on dorso-basal portion of caudal fin. Pectoral fin hyaline, pelvic fin white.

Hermaphrodites. Flank dark brownish grey, with horizontal rows of pale silver or pale golden spots on entire flank; nearly rounded, black blotch on humeral region. Dorsum greenish brown, venter white. Head side and jaws brownish grey. Iris brown. Unpaired fins hyaline, with dark grey dots on basal portion of dorsal and caudal fins; distal margin of anal fin and ventral margin of caudal fin often with narrow light grey band, subdistal portion of anal fin pale yellow; round black spot with yellowish white margin on dorso-basal portion of caudal fin. Paired fins hyaline.

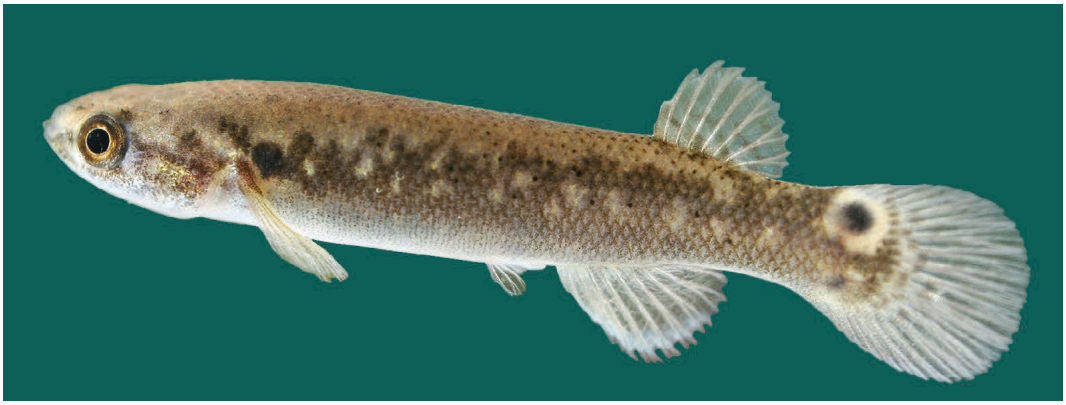

Fig. 4. *Kryptolebias marmoratus*, UFRJ 6633, hermaphrodite, 31.5 mm SL; Brazil: Rio Grande do Norte: Guamaré.

Geographical distribution. *Kryptolebias ocellatus* is endemic to south-eastern and southern Brazilian coast (Fig. 2). It is recorded from an area between the mangroves of the inner part of the Guanabara bay, in Rio de Janeiro state (22°40'28"S 43°03'40"W) and the Tubarão river, Santa Catarina state (28°31'16"S 48°50'47"W). It is sympatric with *K. hermaphroditus* in localities within the Guanabara and Sepetiba bays. Frequently found in brackish water channels and streams banks associated to mangroves, sometimes in saltwater among roots of typical mangrove trees.

Male occurrence and colour pattern frequency. Males were found in all localities sampled, nearly as numerous as hermaphrodites. The dark morph was most common in all populations except in the Tubarão river mouth, where only representatives of the light morph were found. The light morph was rare in the Guaratiba mangrove, corresponding to about 1 % of all male samples together, but common in the Divinéia mangrove, about 20 %, and very common in the Linguado channel mangrove, about 50 %.

Kryptolebias marmoratus (Poey, 1880)
(Fig. 4)

Rivulus marmoratus Poey, 1880: 248 (lectotype: USNM 37429, designated by Rivas, 1945; type locality: Cuba).

Rivulus heyei Nichols, 1914: 143 (holotype: AMNH 5069; type locality: Saona Island at eastern extremity of Haiti).

Rivulus marmoratus bonairensis Hoedeman, 1958: 117 (holotype: ZMA 100436; type locality: Pos di Pepe, Bonaire).

Rivulus garciai Cruz & Dubitsky, 1976: 4 (holotype: IZAC uncat.; type locality: swamps in Varadero, Matanzas, Cuba).

Material examined. All from north-eastern Brazil. UFRJ 6633, 1; UFRJ 6634, 5; UFRJ 9288, 2; Estado do Rio Grande do Norte: mangrove near Guamaré, 5°06'46"S 36°20'42"W; W. J. E. M. Costa & C. P. Bove, 9 May 2008. – MNHN 1991-0367, 2; Estado de Pernambuco: pools near sea, Recife, 8°02'17"S 34°51'51"W; J. Huber, Aug 1981. – MZUSP 38363, 1; Estado de Alagoas: Maceió, 9°40'52"S 35°45'36"W; no data on collection. – MCP 12820, 5; Estado de Alagoas: Mundaú mangrove, 9°39'18"S 35°47'05"W; R. L. Teixeira, 15 Jun 1988.

Colouration. Hermaphrodites. Flank dark brownish grey, with horizontal rows of light brown spots; nearly rounded black blotch on humeral region. Round black spot with yellowish white margin on postero-dorsal portion of caudal peduncle. Dorsum pale brown, venter white. Head side and jaws brownish grey. Iris brown. Unpaired fins hyaline, with dark grey dots on basal portion; distal margin of anal fin bluish white. Paired fins hyaline.

Geographical distribution. *Kryptolebias marmoratus* has been recorded from a huge geographical area in the northern hemisphere, including Antilles, eastern coast of Central America, southern North America, Bahamas, and northern South America. In the southern hemisphere, it is herein first recorded from northeastern Brazilian coastal plains. At least in the Guamaré mangrove, the

only locality sampled by the author, *K. marmoratus* was collected in a marine mangrove habitat close to the sea.

Male occurrence. No male was present in populations of *K. marmoratus* inhabiting the South Atlantic coast here listed.

Discussion

Colouration and taxonomy. Costa (2011) distinguished *K. hermaphroditus* from its sister group species, *K. marmoratus*, by a single colour pattern character of hermaphrodites, comprising the presence of longitudinal rows of pale silver to pale gold small spots restricted to the dorsal portion of the flank in *K. hermaphroditus*, contrasting with numerous pale silver spots scattered over the entire flank. However, this character is difficult to analyse, since preserved specimens exhibit more spots than those visible in live specimens, making distinction subjective. Other characters of the colour pattern of hermaphrodites may be informative in distinguishing these species, including a larger humeral spot in *K. hermaphroditus*, slightly larger than the orbit and the caudal spot (vs. humeral spot approximately equal in size to caudal spot, and smaller than orbit in *K. marmoratus*) and a constant gradual transition between the colour of the flank and that of the dorsum in *K. hermaphroditus* (vs. in specimens exposed to sun light, a sharply marked difference between the darker flank and the lighter dorsum) (compare Figs. 1 and 4), but some variability may occur along the huge geographical distribution of *K. marmoratus*.

Male colouration in *K. hermaphroditus* provides some diagnostic colour pattern characters making possible an easier distinction from *K. marmoratus*. The caudal fin in males of *K. hermaphroditus* always has a broad black margin along the whole fin, bordered by a broad sub-marginal white zone, a pattern never recorded for *K. marmoratus*. In the last species, the caudal fin is yellowish orange, often without distinctive concentration of melanophores on fin margins, but sometimes bearing a narrow black stripe on the ventral margin of the fin, or sometimes another one on the dorsal margin, more concentrated in the posterior corners of the fin, but not extending over the middle portion of the posterior margin (e.g., Davis et al., 1990). Moreover, males of *K. marmoratus* have an intense orange pigmentation on the ventral portion of the trunk and head (e.g., Harrington, 1967, 1971; Davis et al., 1990; Soto & Noakes, 1994), a colour pattern not found in any male of *K. hermaphroditus*. However, males are usually rare in both *K. hermaphroditus* and *K. marmoratus*, with many collections containing only hermaphrodites. In this case, identification of these populations would be possible using hermaphrodite characters listed above or using molecular data (Tatarenkov et al., 2009; Costa, Mattos & Amorim, unpublished). In addition, adult specimens of *K. hermaphroditus* above 35 mm SL, both males and hermaphrodites, have a long snout, longer than the orbit, contrasting with the short snout in other species of mangrove killifishes, with the snout being shorter than the orbit, but a study containing larger samples of *K. marmoratus* is needed to confirm the usefulness of this character.

Kryptolebias ocellatus has some features of the male colour pattern similar to those found in *K. hermaphroditus* (compare Figs. 1 and 3), as the possession of a broad black marginal stripe and a light sub-marginal zone on the caudal fin, although not being sister species (Costa, Mattos & Amorim, unpublished). On the other hand, the presence of a black spot on the dorsal portion of the caudal-fin base in larger adult males make the colour pattern of *K. ocellatus* readily distinguishable from the other species of the *K. marmoratus* group, in which that spot is present in hermaphrodites and juvenile males, but lost or sometimes vestigial in adult males.

The presence of two colour morphs here described for both *K. hermaphroditus* and *K. ocellatus* has not been recorded for *K. marmoratus* and other rivulid killifishes. On the other hand, a very similar condition has been described for African nothobranchiids, with two distinctive colour morphs occurring in single populations (e.g., Costa, 2009; Reichard et al., 2009). However, it is not possible yet to assess the evolutionary role of sympatric different colour morphs, as well as the origin of this uncommon condition among different lineages of aplocheiloid killifishes is still unknown.

Geographical distribution of the *K. marmoratus* group in southern Atlantic coastal plains. The present study indicates that *K. marmoratus* occurs along the north-eastern Brazilian coastal

plains, with the southern-most record in Maceió (9°40'52"S 35°45'36"W), whereas *K. hermaphroditus*, its closest relative, is endemic of south-eastern Brazil, south of Coqueiral beach (19°56'05"S 40°07'49"W). The gap of about 1100 km between the geographical distribution of these two species (Fig. 2) may not be explained by insufficient sampling, since sporadic collections made by the author in several well preserved estuarine areas failed in obtaining any specimen of mangrove killifishes. Historical factors determining the present distribution of these species are still unknown, although a recent dispersal of the most recent ancestor of *K. marmoratus* from south-eastern South America to the northern hemisphere has been implicitly assumed (Turner et al., 2006).

Whereas *K. hermaphroditus* is found in shallow brackish water channels of estuarine zones, usually associated to mangroves, often in places protected by terrestrial marginal plants, sometimes in freshwater streams within dense Atlantic rain forest, *K. marmoratus* has been reported to occur in Caribbean mangrove areas under direct influence of seawater, often hidden in crab burrows (Taylor, 1988, 1992, 2012; Davis et al., 1990). In northeastern Brazil, *K. marmoratus* was found in a mangrove habitat similar to that reported for the Caribbean coast, whereas *K. hermaphroditus* was never found in this kind of habitat. These data indicate that *K. hermaphroditus* and *K. marmoratus* prefer different habitats, although the latter species tolerating a broad array of ecological factors (e.g., Davis et al., 1990). On the other hand, *K. ocellatus* is found both in brackish channels and mangroves zones under direct seawater influence.

Kryptolebias ocellatus occurs both in southern and south-eastern Brazilian coastal plains, having its distribution area highly overlapping with the area occupied by *K. hermaphroditus* in Guanabara and Sepetiba bays, south-eastern Brazil, where the two species are commonly sympatric (Fig. 2). Whereas *K. hermaphroditus* is relatively rare in its habitat, always with 20 or less specimens found in each collection, *K. ocellatus* is very common, with over 100 specimens easily collected at a single locality at every field collection. However, the relative rareness of *K. hermaphroditus* does not seem a result of the sympatric occurrence of *K. ocellatus*, since similar field data were obtained both in sympatric conditions and when *K. hermaphroditus* was found alone.

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