

Description of a new *Heros* species (Teleostei, Cichlidae) from the Rio Orinoco drainage and notes on *Heros severus* Heckel, 1840

Beschreibung einer neuen *Heros*-Art (Teleostei, Cichlidae) aus dem
Rio Orinoco-Einzug und Anmerkungen zu *Heros severus* Heckel, 1840

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Summary: *Heros liberifer* sp. n. is described from the drainage of the upper and middle Rio Orinoco in Venezuela. The new species is distinguished from all other *Heros* species by its unique colouration pattern of several horizontal series of tiny bright red dots on the lower half of the body sides and by its unusual brood care. *Heros liberifer* sp. n. can be distinguished from the syntopic *Heros severus* Heckel, 1840 by a distinct caudal spot, narrower lips, a bright red iris and the 4th vertical bar, which is not shortened, but extends from the anal fin base to the base of the dorsal fin. In addition, comments are made on the colouration of live specimens of *Heros severus*, its distribution and ecology.

Key words: *Heros*, reproductive behaviour, Cichlinae.

Resumen: Se describe una nueva especie de cíclido, *Heros liberifer*, de la cuenca del alto y medio río Orinoco en Venezuela. La nueva especie se distingue de todas las demás especies del género *Heros* por su patrón de colouración única con varias series horizontales de pequeños puntos rojos brillantes en la mitad inferior de los laterales del cuerpo y por su tipo de cuidado parental. *Heros liberifer* sp. n. puede distinguirse de la especie sintópica *Heros severus* HECKEL, 1840 por la siguiente combinación de características: una mancha caudal distinta, labios estrechos, un iris de colour rojo brillante y la cuarta barra vertical no reducida, que se extiende desde la base de la aleta anal a la base de la aleta dorsal. Además, se hacen comentarios a la colouración de los especímenes vivos de *Heros severus*, su distribución y ecología.

Palabras clave: *Heros*, comportamiento reproductivo, Cichlinae.

Zusammenfassung: *Heros liberifer* sp. n. wird aus dem Einzugsgebiet des oberen und mittleren Orinoco in Venezuela beschrieben. Die neue Art unterscheidet sich von allen anderen *Heros*-Arten durch ihr einzigartiges Farbmuster in der unteren Hälfte der Körperseiten, das aus mehreren horizontalen Reihen winziger, kräftig roter Pünktchen besteht, und die Form der Brutpflege. *Heros liberifer* sp. n. lässt sich von der syntopen Art *Heros severus* HECKEL, 1840 durch einen deutlichen Schwanzwurzelfleck, schmalere Lippen, die leuchtend rote Iris und den 4. Querbalken unterscheiden, der nicht verkürzt ist, sondern sich von der Afterflossenbasis bis zur Rückenflossenbasis erstreckt. Zusätzlich werden Anmerkungen zur Lebendfärbung, Verbreitung und Ökologie von *Heros severus* gemacht.

Schlüsselwörter: *Heros*, Fortpflanzungsverhalten, Cichlinae.

1. Introduction

The South American cichlid genus *Heros* was erected by HECKEL (1840) in order to describe 13 heroine cichlid species from South and

Central Amerika. Among them were the five nominal species *Heros severus* and *H. efasciatus*, both from the Rio Negro, and *H. spurius*, *H. coryphaeus* and *H. modestus* from the Rio Guaporé.

REGAN (1905) treated *Heros* as a section of the then catch-all genus *Cichlasoma* SWAINSON and recognised only *Cichlasoma severus* as a valid species. But in 1983 KULLANDER resurrected *Heros* as a monotypic genus with *Heros severus* as sole species taxon. Later he gave a revised diagnosis of the genus and redescribed *Heros appendiculatus* (Castelnau, 1855) from the Ucayali (KULLANDER 1986). At present, the alpha taxonomy of the genus is by far not resolved because there are several nominal species for which no adequate diagnoses are available (KULLANDER 1986, 2003).

In the latest taxonomic treatment of the genus KULLANDER (2003) synonymised *Heros appendiculatus* with *H. efasciatus* and recognized four taxa as valid, *Heros severus* Heckel, 1840, *H. spurius* Heckel, 1840, *H. efasciatus* Heckel, 1840 and *H. notatus* (Jardine, 1843). He indicated that the status of other nominal taxa needs further analysis. Apparently more species exist, for since the end of the last century commercial imports and collections by aquarists have yielded *Heros* specimens which clearly depart in their bar patterns or other characteristics from the known taxa (STAWIKOWSKI & WERNER 1988, 1998, STAECK 2009).

In the redescription of *Heros appendiculatus* KULLANDER (1986) distinguished it from *H. severus*, the type species of the genus, and listed diagnostic features. He stated that the distinctness of the two species was clear because *Heros severus*, distributed “in the upper R. Negro and upper R. Orinoco, is much more slender, has a distinct caudal spot [...], distinct vertical bars [...] and narrower lips.” This diagnosis perfectly applies to a fish, which at least since 1992 (see STAECK & LINKE 1994, STAWIKOWSKI & WERNER 1995) has repeatedly been exported as aquarium fish from the Orinoco drainage and since then has been well known among aquarists. In 1994 this *Heros* unexpectedly turned out to be a delayed mouthbrooder, which is apparently unique in the genus (STAWIKOWSKI 1994, STAWIKOWSKI & WERNER 1995).

STAWIKOWSKI (1994) recognized the similarities between the mouthbrooding species and the characteristics given for *Heros severus* by KULLANDER (1986). Later KULLANDER confirmed

that the mouthbrooder is the “real *Heros severus*” (STAWIKOWSKI 1994). At that time KULLANDER’s (1986) characterisation of *Heros severus* and his answer to STAWIKOWSKI were considered sufficient evidence for a reliable determination. Consequently, the mouthbrooding *Heros* from the Orinoco has commonly been thought to be *Heros severus* since then (e.g. STAECK & LINKE 1994; STAECK 2009, STAWIKOWSKI & WERNER 1995, 1998).

The view that the mouthbrooding cichlid is *Heros severus* was recently challenged in an aquaristic publication (DITTRICH 2014). The examination of the holotype of *H. severus* by the first author confirmed that it is not identical with the mouthbrooding species, because both differ in several characteristic features (see diagnosis and discussion). The purpose of this paper is to present new information on the diagnostic characters of *H. severus* and to provide the formal description of the species that is repeatedly mentioned as a mouthbrooder in aquaristic publications and since almost two decades has been misidentified as *H. severus*.

2. Material & methods

The type specimens were fixed in 75% ethanol. The holotype and paratypes are deposited in the fish collections of the Museum für Tierkunde Dresden (MTD F) and the Naturhistorisches Museum Wien (NMW). Additional material deposited in the Museum für Naturkunde in Berlin (ZMB) was also examined.

The techniques for taking measurements and meristic data follow those described in KULLANDER (1983, 1986) and KULLANDER & NIJSSSEN (1989). Measurements were made with an electronic digital caliper reading to the nearest 0.1 mm and with a measuring tape to the nearest mm when the distance was more than 130 mm. Specimen lengths are given as standard length (SL) or total length (TL). Scale rows are numbered as described by KULLANDER (1990), i. e. the row above the lower lateral line is labelled E1. Numbers in brackets after counts indicate the number of specimens examined with that result. The terminology of vertical bars follows

KULLANDER & SILFVERGRIP (1991), for their numbering facilitates the description of the vertical bars and enables an easier comparison of species. According to this way of counting, the caudal spot corresponds to bar 1. The species concept used here is the diagnostic variant of the phylogenetic species concept advocated by NIXON & WHEELER (1990).

Beside the data obtained from the examined material (listed below), information from previously described and redescribed species (viz. HECKEL 1840, JARDINE 1843, CASTELNAU 1855, COPE 1872, KULLANDER 1986, and SCHINDLER & STAECK 1997) were also used. Specimens not explicitly registered as type specimens of the new species are non types.

Comparative material examined: *Heros severus*: NMW 17638, holotype, 200 mm SL, Marabitanas, Rio Negro; MTD F 33469, 1, 122.4 mm SL, Rio Casiquiare at junction with Rio Yatúa; MTD F 33470, 1, 30.2 mm SL, small tributary to lower Rio Autana. *Heros liberifer*: not deposited

(collection of the authors), 5, 13.3-126.4 mm SL, Banjo de Aripo, Rio Caura drainage, Estado Bolivar, Venezuela. *Heros notatus*: ZMB 32756, 2, 99.8-113.7 mm SL, Essequibo River, close to Rockstone, Guyana; not deposited (collection of the authors), 5, 58.9-79.5 mm SL, Demerara River drainage, Linden Highway, Guyana; not deposited (collection of the authors), 2, 12-15 cm TL, Essequibo River, Guyana.

3. Results

3.1. *Heros liberifer* sp. nov. (figs 1-6, 8, 10)

Holotype. MTD F 33463, 164 mm SL, Laguna Piranha at right side of lower Rio Manapiare (Rio Ventuari drainage), approx. 3 km downstream from the town of San Juan de Manapiare, Estado Amazonas, Venezuela, (approx. 5° 16' N, 65° 5' W), leg. R. RIETSCH et al., February 2013.

Paratypes. MTD F 33464-33468, 5, 80-102 mm SL, collecting data like holotype; NMW



Fig. 1: *Heros liberifer* sp. n., holotype, male, 164 mm SL, MTD F 33463.

Abb. 1: *Heros liberifer* sp. n., Holotypus, Männchen, 164 mm SL, MTD 33463.



Fig. 2: Topotypic adult male *Heros liberifer* sp. n. (approx. 20 cm TL) in a photo tank immediately after capture.

Abb. 2: Topotypisches adultes Männchen von *Heros liberifer* sp. n. (ca. 20 cm TL) im Fotoaquarium unmittelbar nach dem Fang.



Fig. 3: Adult female *Heros liberifer* sp. n. photographed in aquarium.

Abb. 3: Adultes Weibchen von *Heros liberifer* sp. n. im Aquarium fotografiert.



Fig. 4: Adult female *Heros liberifer* sp. n. guarding eggs in the Pozo Azul some kilometres north of Puerto Ayacucho (underwater photograph).

Abb. 4: Adultes Weibchen von *Heros liberifer* sp. n. beim Bewachen der Eier im Pozo Azul einige Kilometer nördlich von Puerto Ayacucho (Unterwasserfoto).

98370, 2 specimens, 94-109 mm SL, collecting data like holotype.

Diagnosis. *Heros liberifer* differs from all its congeners by a pattern of several horizontal series of bright red dots on the lower half of the body sides (versus no rows of red dots), a distinct caudal spot in adult specimens (versus caudal spot usually merged with bar 2 in adult specimens) and tiny dark dots on operculum and cheeks in adult males (versus large dots or a vermicular pattern). It can be distinguished from adult specimens of the frequently syntopic *Heros severus* by narrow (versus thick) lips, bar 4, which is not shortened, but extends from the anal fin base onto the base of the dorsal fin (versus bar 4 extending only slightly above the lower lateral line), by the first two anterior hemal spines, which are broader and partially connected (versus the first three hemal spines connected), and a bright red (versus brown to dark reddish) iris in live specimens.

Description. Refer to figures 1-5 for general appearance and colour pattern. Morphometric data

of type specimens are given in table 1. Dorsal and anal fin ray counts of types and additional specimens are summarized in table 2.

Description based on type specimens. Body deep, laterally strongly compressed. Snout round in lateral view, somewhat pointed in dorsal view; moderately long. Jaws isognathus. Lips comparatively narrow. Anterior dorsal head profile straight or slightly arched, at nape concave; ventral contours less arched. Prepelvic and abdominal contour straight or slightly arched. Dorsal fin base almost straight. Caudal peduncle with straight dorsal and ventral edge. Dorsal fin and anal fin pointed, elongated, extending to posterior end of caudal fin or slightly beyond in adult specimens. Caudal fin round or slightly subtruncate; caudal fin length about 1/4 to almost 1/3 of SL.

Pectoral fin round with 12 or 13 rays. Pelvic fin with one spine and 5 rays, pointed; pelvic-fin length up to 45% of SL. Dorsal fin XV.12(3), XV.13(1), XVI.12(2) or XVI.13(2). Anal fin VI.10(2), VI.11(4), VI.12(1) or VII.12(1).

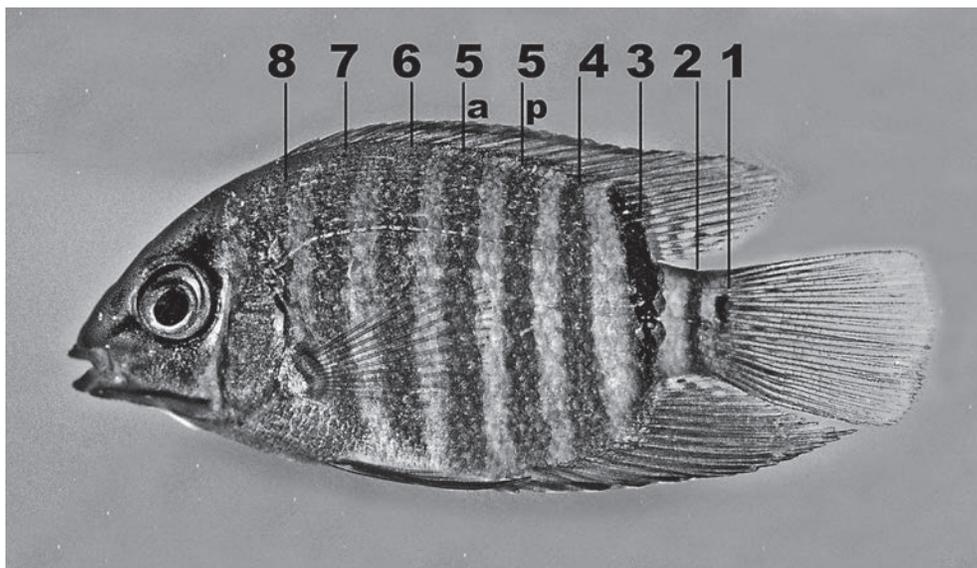


Fig. 5: Juvenile *Heros liberifer* sp. n. with complete pattern of vertical bars immediately after capture in a photographic tank. The numbering follows KULLANDER & SILFVERGRIP (1991). See ŘÍČAN et al. (2005) for development of bars during ontogenesis.

Abb. 5: Subadultes Exemplar von *Heros liberifer* sp. n. mit vollständigem Muster vertikaler Balken im Fotografieraquarium unmittelbar nach dem Fang. Die Nummerierung folgt KULLANDER & SILFVERGRIP (1991). Zur Entwicklung der Balken während der Ontogenese vergleiche ŘÍČAN et al. (2005).

Tab. 1: Measurements of the type specimens of *Heros liberifer* spec. nov. and two specimens of *H. severus* (NMW 17638 and MTD F 33469) in percent of SL (except SL in mm); min = lowest value, max = highest value, mean = arithmetic mean, sd = standard deviation.

Tab. 1: Messwerte der Typenexemplare von *Heros liberifer* spec. nov. und von zwei Exemplaren von *H. severus* (NMW 17638 und MTD F 33469) in Prozent der Standardlänge (außer SL in mm); min = kleinster Wert, max = höchster Wert, sd = Standardabweichung.

	<i>H. liberifer</i>				<i>H. severus</i>	
	min	max	mean	sd		holotype
Standard length (mm)	80	164	104		122	200
Total length	129,5	135,4	133,2	2,28	136,0	131,2
Head length	32,2	35,4	33,9	1,07	32,3	32,6
Snout length	9,4	14,6	12,2	1,89	10,7	9,8
Body depth	49,9	59,6	54,7	2,83	58,6	52,4
Orbital diameter	8,8	10,4	9,5	0,56	9,0	8,4
Interorbital width	11,7	14,6	12,9	0,89	13,3	--
Prcorbital depth	10,1	14,6	11,5	1,37	10,1	10,3
Cuadal peduncle depth	17,9	19,2	18,3	0,49	17,1	16,8
Cuadal peduncle length	5,4	7,5	6,5	0,80	6,0	7,7
Pectoral fin length	28,3	30,1	29,3	0,61	30,3	--
Pelvic fin length	31,9	40,9	35,1	2,65	41,1	--
Dorsal fin base length	61,2	63,8	62,5	0,94	65,4	64,1
Anal fin base length	34,7	38,8	36,6	1,22	40,4	40,2
Last dorsal spine length	17,1	20,9	18,8	1,37	20,3	--

Tab. 2: Dorsal fin and anal fin count frequencies of four *Heros* species. Data of *H. liberifer* spec. nov. include types and additional examined specimens, data of *H. notatus* from SCHINDLER & STAECK (1997), data of *H. efasciatus* from KULLANDER (1986), and data of *H. severus* from examined specimens (including holotype). An asterisk indicates the value of the primary type specimen. Modal value of each species is printed in bold.

Tab. 2: Zählwerte der Rücken- und der Afterflossen von vier *Heros*-Arten. Die Angaben für *H. liberifer* spec. nov. enthalten die Werte des Holotypus und des zusätzlichen Materials; die Daten für *H. notatus* sind SCHINDLER & STAECK (1997) entnommen und die für *H. efasciatus* aus KULLANDER (1986); Angaben für *H. severus* entstammen dem untersuchten Material (einschließlich Holotypus). Ein Sternchen hinter der Ziffer zeigt den jeweiligen Zählwert des primären Typusexemplars an. Der Modalwert der einzelnen Arten ist fett gedruckt.

Dorsal fin spines	XIV	XV	XV	XV	XVI	XVI	XVI
Dorsal fin rays	13	12	13	14	12	13	14
<i>H. liberifer</i>	1	5*	3		2	2	
<i>H. severus</i>						3*	
<i>H. notatus</i>				1		5	3
<i>H. efasciatus</i>			1	4	3	19*	

Anal fin spines	VI	VI	VII	VII	VII	VII	VII	VIII	VIII	VIII
Anal fin rays	11	12	10	11	12	13	14	11	12	13
<i>H. liberifer</i>	7*	3	1	2						
<i>H. severus</i>					3*					
<i>H. notatus</i>						4	4			1
<i>H. efasciatus</i>						5*		4	14	4

Predorsal scales smaller than scales of body flanks, irregularly arranged. Cheek scales in 4(1), 5(6), or 6(1) rows. Dorsal and anal fin bases densely scaled, with up to 5 rows of small scales between fin rays. Pelvic and pectoral fin naked. Caudal fin base densely scaled, on its dorsal and ventral parts to a third, centrally to a fourth of caudal fin length. Scales in E1 row 27(4), 28(3) or 29(1). Scales on upper lateral line 17(1), 18(3), 19(3) or 20(1); scales in lower lateral line 11(1) or 12(7), including two scales on caudal fin. Upper tube-series on caudal fin with up to eleven scales between rays D2 and D3; ventral branch with up to 15 scales between V4 and V5, longer than dorsal branch. First gill arch with two gill rakers on epibranchial, one in angle, and 9(4), 10(2) or 11(2) externally on ceratobranchial.

Lower pharyngeal tooth plate (in a 99 mm SL specimen, dissected) densely toothed, wider than long (width about 110% of its length); 13/14 teeth in posterior row, and 9/10 teeth in median row (values for left and right side). Medioposterior teeth largest; teeth gradually decreasing in length in rostral and lateral direction; few anterior teeth unicuspid, remainder bicuspid. Microgill rakers externally on ceratobranchial 2-4; ceratobranchial 1 with tooth plates. Jaw teeth subconical with slightly recurved tips. In upper jaw hemiseries 12-16(3) outer row teeth,

in lower jaw hemiseries 12-17(3). First two to three teeth in outer row next to symphysis longest, in larger specimen with an indistinct second cusp. Teeth posteriorly decreasing in size; teeth in inner rows much smaller. In holotype 13+14 vertebrae.

Colouration of live specimens (figs 2-6). Based on observations immediately after capture, on underwater observations in the habitat and on specimens kept in the aquarium. Adult specimens colourful with a pattern of narrow horizontal red lines on the lower half of the body; without dark or iridescent head markings. Head and body uniformly pale yellowish grey or light greenish. With nine dark brown to blackish vertical bars between the eye and the caudal fin: bar 1 reduced to a small caudal spot separated from bar 2 and positioned slightly dorsal to lower lateral line; bar 2 across posterior end of caudal peduncle; bar 3 prominent, darker than the others, slightly extending onto dorsal and anal fin base; bar 4 from base of soft dorsal fin to base of soft anal fin; bar 5 vertically split into an anterior and a posterior part, both reaching from base of spinous anal fin to base of spinous dorsal fin; bar 6 between middle of belly and dorsal fin; bar 7 between pectoral axilla and dorsal fin, slightly slanting, continued ventrally between pectoral axilla and belly slightly poste-

Fig. 6: Underwater photograph of a young *Heros severus* (in the centre) and two *H. liberifer* in a tributary blackwater creek of the lower Rio Autana. **Abb. 6:** Unterwasserfoto eines jungen *Heros severus* (in der Mitte) und zweier *H. liberifer* in einem kleinen Schwarzwasserzfluss des unteren Rio Autana.



rior to pelvic fin origin; bar 8 indistinct, between dorsal fin origin and operculum, slightly slanting. No lateral band and no midlateral spot present. Dorsal fin light grey to smoky, soft portion hyaline with light spots in cross series and a basal black extension of bar 3. Anal fin like dorsal fin, soft part hyaline, last few membranes lighter with dark dots. Caudal fin hyaline or smoky with irregular series of small light dots. Pelvic fins grey or with reddish tinge. Pectoral fins hyaline and colourless.

On the lower body sides each scale with a bright red centre. The red dots form a pattern of regular horizontal series, which may often extend from the ventral regions to the upper lateral line. It is particularly prominent in adult specimens. Iris bright red. Dark stripe along lower jaw, continued on preoperculum. Adult males with minute dark brown dots scattered over most of the lower regions of cheek and operculum.

Underwater observations in the natural habitats revealed that subadult specimens in neutral colouration usually are uniformly pale yellow with only bar 3 pronounced (fig. 6). Adult specimens frequently show more vertical bars (fig. 4).

Colouration in alcohol (fig. 1). Body uniformly brown, head and fins greyish. Vertical bars and dark pattern on fins as described above. Bars distinct; bar 3 black, very prominent, the others dark brown. In one paratype bar 4 vertically split into an anterior and posterior part. Without lateral band and lateral spot. All red pigmentation faded and discoloured. Supraorbital spot dark, postorbital spot blackish, more prominent. Dark greyish stripe from anterior margin of orbital to mouth. Grey stripe along lower jaw, continued on preoperculum, not conspicuous. No suborbital stripe in adult specimens.

Sexual dimorphism. There are no obvious external sex differences in fin length or intensity of the colour pattern. Adult males, however, with minute dark brown dots scattered over most of the lower regions of cheek and operculum. Females usually without such dots (figs 1-3).

Reproductive behaviour. Observations under aquarium conditions showed that *H. liberifer* is a monogamous delayed biparental

(larvophile) mouthbrooder (STAWIKOWSKI 1994, STAWIKOWSKI & WERNER 1995). Like its congeners, *H. liberifer* starts reproduction like a substratum spawner and deposits the eggs on a vertical or sometimes on a horizontal surface. At a water temperature of 27 °C hatching occurs approximately forty hours post spawning. Then both parents pick up the larvae in order to brood them orally. The fry attempt swimming three or four days later. The male and female fish practice long-term biparental defense of their mobile fry and both share all the duties of brood care, which may last up to three weeks. A detailed description of the reproductive behaviour was published by STAWIKOWSKI & WERNER (1995, 1998).

Geographical distribution and ecological notes. *Heros liberifer* is widely distributed in the basin of the upper and middle Rio Orinoco. The exact distribution, however, is documented only incompletely. In particular the western boundaries of its occurrence are not known because the left side tributaries of the Rio Orinoco in Columbia are poorly sampled due to the difficult political situation in these regions during the last decades.

In the north we collected *H. liberifer* at the Banjo of Aripao (cf. photo of a specimen in STAECK & LINKE 1995). This collecting site located in the southeast of the town of Maripa belongs to the drainage of the Rio Caura, a tributary of the middle Rio Orinoco. In the south we found this species in the lower Rio Casiquiare near the village of El Niñal at the mouth of the Rio Pasimoni. In the east of the Estado Amazonas we caught *H. liberifer* in the Laguna Piranha (type locality) on the right bank of the upper Rio Manapiare (tributary to upper Rio Ventuari) a few kilometres downstream from the town of San Juan de Manapiare. Additional collecting sites are in the lower Rio Atabapo, in the drainage of the lower Rio Autana and in the Pozo Azul some kilometres north of Puerto Ayacucho. Several of our collecting sites were independently confirmed by STAWIKOWSKI & WERNER (1995, 1998).

Underwater observations revealed that *H. liberifer* is a lentic-adapted species and that its

typical biotopes are flooded forest habitats. As the seasonal fluctuation in water level is considerable in the Rio Orinoco drainage, in the highwater season the river water floods into the riparian forest and inundates the vegetation. The deep and high shape of the laterally strongly compressed body of *H. liberifer* is apparently an adaptation to these floodwater habitats. The fishes breed in the flooded riparian forest during the flood season.

However, at the beginning of the dry season, the water level rapidly falls and the river water returns into its main channel. At this time, the fishes have to leave the riparian forests, which mostly dry up, and spend the low-water season among submerged logs, trunks and branches, which in the proximity of the banks fell into the river. Many stretches of the Rio Atabapo are characterized by large granite boulders. Our underwater observations revealed that during the lowwater season *H. liberifer* frequently seeks shelter in the crevices and gaps found between the boulders.

Our findings indicate that *H. liberifer* apparently has no narrow habitat requirement. As we observed this species not only in clearwater and extreme blackwater habitats, but also in whitewater habitats, it is capable of dealing with a wide range of physicochemical environmental conditions (pH 4.1-6.1; conductivity 4-15 $\mu\text{S}/\text{cm}$).

Etymology. The species epithet is a combination of the Latin words *liberi* (= children) and *ferre* (= to carry). It is a noun in apposition and refers to the oral incubation, a reproductive behaviour, which is apparently unique in the genus.

3.2 Notes on *Heros severus* HECKEL, 1840

The type specimen (figs 7, 9, 11). In respect to its old age the holotype of *Heros severus* is in good condition although the pigmentation has faded and several scales are missing. Body sides, head and fins uniformly light brown. Pattern of vertical bars still distinct. Bar 4 shortened, more pronounced on the right-hand than on the left-hand side. The lips are comparatively thick. No caudal peduncle spot (bars 1 and 2 fused).

Vertebrae 13+15. See table 1 for morphometric data and table 2 for dorsal and anal fin counts.

Colouration of live specimens (figs 6, 12-13). Based on observations immediately after capture, on underwater observations in the habitat and on specimens from the Rio Casiquiare kept in the aquarium. Body of adult specimens uniformly pale yellow, head greenish, chest dark red. Small maroon to reddish spots scattered over gill cover, lower region of head and anterior sides of body. Iris brown or dark reddish. On lower preoperculum a dark stripe between its posterior border and mouth.

With eight dark brown to blackish vertical bars between eye and caudal fin: No separate caudal spot; bar 1 and bar 2 fused, positioned on posterior end of caudal peduncle; bar 3 from soft anal-fin base to soft dorsal fin, darker than the others; bar 4 shortened, commonly reaching only to the lower or at the most to the upper lateral line; anterior and posterior part of bar 5 from base of spinous anal fin to base of spinous dorsal fin; bar 6 between middle of belly and dorsal fin; bar 7 between pectoral axilla and dorsal fin slightly slanting, continued ventrally between pectoral axilla and belly slightly posterior to pelvic fin origin; bar 8 indistinct, between dorsal fin origin and operculum, slightly slanting, continued on chest as stripe from pelvic fin to suboperculum. Super- and suborbital stripe pronounced only in subadult specimens.

Underwater observations in the natural habitats revealed that in juvenile specimens usually all the bars are distinctly visible, even in neutral colouration (fig. 6).

Dorsal fin light grey to smoky, posterior part of soft portion with maroon spots in cross-series. Anal fin smoky with reddish tinge, last membranes of soft part light green with two or three series of maroon dots. Caudal fin hyaline or smoky. Pelvic fins dark with reddish tinge and blackish anterior margin. Pectoral fins hyaline and colourless.

Geographical distribution and ecological notes. *Heros severus* occurs in both the upper Rio Negro basin and the upper Orinoco basin. Collecting sites in the Rio Negro are situated in Brazil in the vicinity of Marabitanas, at São

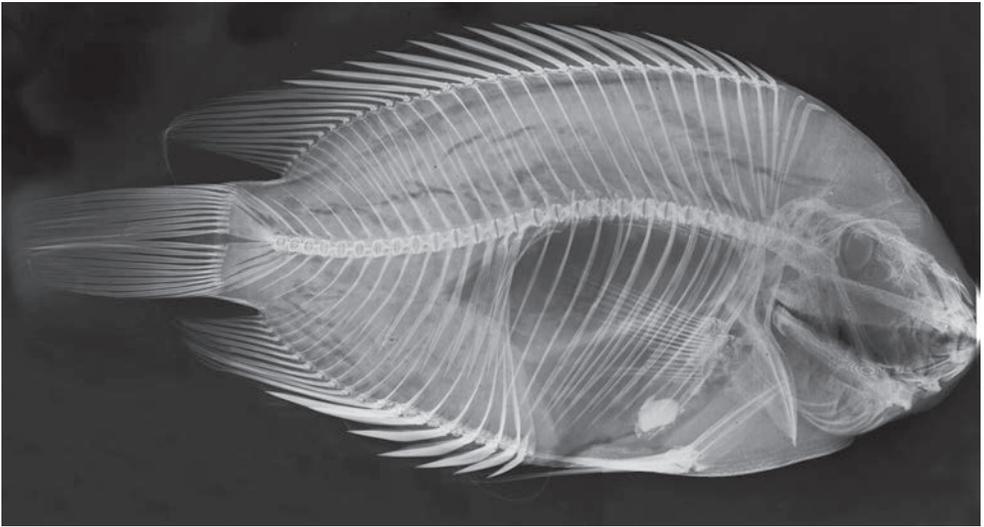


Fig. 7: X-ray photo of holotype of *Heros severus* (NMW 17638). The first three anterior hemal spines are connected. Photo NMW.

Abb. 7: Röntgenaufnahme vom Holotypus von *Heros severus* (NMW 17638). Die ersten drei vorderen Hämalfortsätze sind miteinander verbunden. Photo NMW.

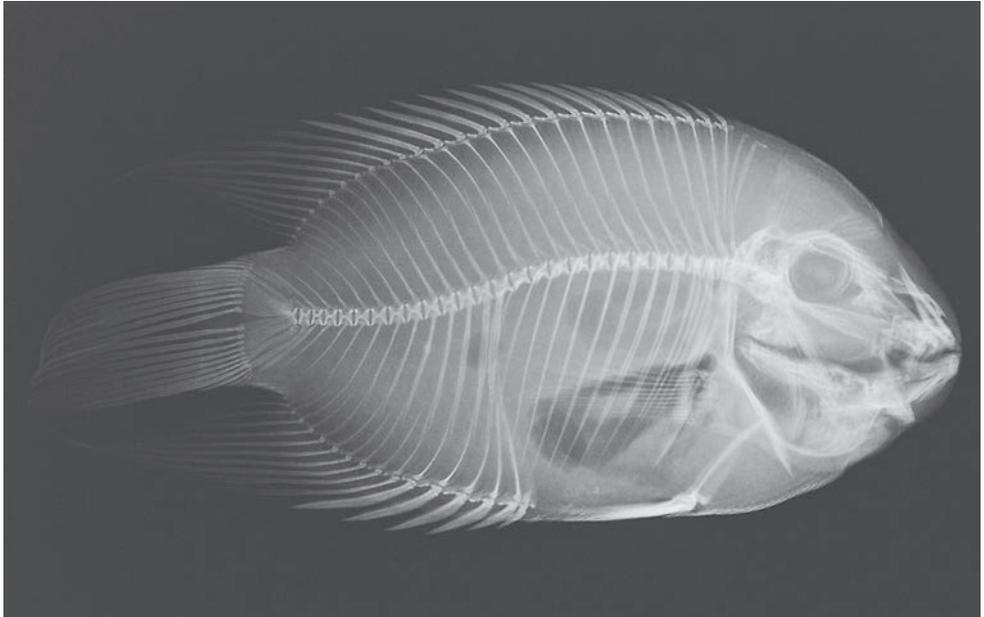


Fig. 8: X-ray photo of holotype of *Heros liberifer* (MTD F 33463). The first two anterior hemal spines are partially connected. Photo Kai S. RÖDIGER.

Abb. 8: Röntgenaufnahme vom Holotypus von *Heros liberifer* (MTD F 33463). Die ersten beiden vorderen Hämalfortsätze sind teilweise miteinander verbunden. Foto Kai S. RÖDIGER.



Fig. 9: Frontal view of holotype of *Heros severus* (NMW 17638): The lips are thicker than in *H. liberifer* (cf. fig. 10).
Abb. 9: Frontalansicht des Holotypus von *Heros severus* (NMW 17638): Die Lippen sind dicker als bei *H. liberifer* (vergleiche Abb. 10).



Fig. 10: Frontal view of holotype of *Heros liberifer*.
Abb. 10: Frontalansicht des Holotypus von *Heros liberifer*.



Fig. 11: The right side of the holotype of *Heros severus* (NMW 17638) shows the shortened bar 4 better than the left side.
Abb. 11: Die rechte Seite des Holotypus von *Heros severus* (NMW 17638) zeigt den verkürzten Querstreifen 4 besser als die linke.



Fig. 12: Adult male *Heros severus* (approx. 15 cm TL, photographed in aquarium) from the Rio Casiquiare.

Abb. 12: Adultes Männchen von *Heros severus* (ca. 15 cm TL, fotografiert im Aquarium) aus dem Rio Casiquiare.



Fig. 13: Juvenile *Heros severus* (approx. 10 cm TL, photographed in aquarium) from the lower Rio Casiquiare near the village of El Niñal at the mouth of the Rio Pasimoni.

Abb. 13: Junger *Heros severus* (ca. 10 cm TL, fotografiert im Aquarium) aus dem unteren Rio Casiquiare nahe des Dorfes El Niñal an der Mündung des Rio Pasimoni.

Gabriel da Cachoeira and close to the mouth of Rio Uaupés (RÖMER 1996, 1998, WARZEL 2003). In Venezuela the occurrence is documented for the lower Rio Casiquiare, the Rio Atabapo and an unnamed tributary creek of the lower Rio Autana (STAECK 2009 and unpublished data). At all these collecting sites typical blackwater conditions exist. These observations suggest that *Heros severus* is a blackwater adapted or even blackwater restricted species. At the above mentioned collecting sites in Venezuela *H. severus* occurs syntopic with *H. liberifer*, but its occurrence is remarkably less abundant than that of its congener.

4. Discussion

4.1. Comparative notes

The species level taxonomy of the genus *Heros* is not completely clarified (KULLANDER 1986, 2003). Therefore, a comparative discussion of the taxa considered as valid by KULLANDER (2003) seems appropriate.

The holotype of *H. efasciatus* is a deep-bodied (55% of the SL) adult male, which now has lost all its dark pigmentation. According to Heckel (1840) the fish originally possessed a dark dot on each scale of the flanks, a pattern which

does not exist in *Heros liberifer*. Furthermore, *H. efasciatus* (cf. KULLANDER 1986, HECKEL 1840) neither possesses the red dots on the lower half of the body sides nor a distinct caudal spot, both diagnostic characters of *H. liberifer*.

KULLANDER (1986, 2003) treated *Chromys appendiculata* Castelnau, 1855, *Chromys fasciata* Castelnau, 1855, *Uaru centrarchoides* Cope, 1872, and *Cichlasoma severum perpunctatum* Miranda Ribeiro, 1918 as synonyms of *Heros efasciatus*. After careful consideration of the original descriptions of these species group taxa we agree with this view.

Besides the character states mentioned in the diagnosis, adult males of *Heros notatus* can be distinguished from *H. liberifer* by the possession of dark dots on the scales on its flanks and the change of bar 4 to 7 into 4 vertical blotches on the ventral part of the body sides (JARDINE 1843, SCHINDLER & STAECK 1997).

Heros spurius, *H. coryphaeus* and *H. modestus* were described from the Rio Guaporé drainage. As the description of the three taxa is based on different life stages or sexes of the same species (personal observation) we agree with KULLANDER (2003), who synonymised them – following the first revisor (GÜNTHER 1862) – with *H. spurius*. *Heros liberifer* differs from *H. spurius* by the lack of dark dots on the flank scales in adult males and by the characters states given in the diagnosis.

In addition to the differences described in the diagnosis, *H. liberifer* is distinguished from the frequently syntopic species *H. severus* by a lower number of dorsal and anal fin rays (tab. 2) and by its brood care as a delayed biparental (larvophile) mouthbrooder, a form of reproductive behaviour so far not observed in other *Heros* species.

4.2. Type specimen of *Heros severus*

Both KULLANDER (2003) and ESCHMEYER (2015) regard (with question marks) the following specimens as possible syntypes of *Heros severus*: NMW 17354, NMW 17638 and NMW 17656. However, according to HECKEL's description (1840) there can be no doubt that he used only one specimen. The examination of the handwritten catalogue in NMW reveals that NMW

17354 is a type specimen of *Heros modestus* Heckel, 1840 and that NMW 17656 is a type specimen of *H. spurius* Heckel, 1840. Consequently, the holotype of *Heros severus* is NMW 17638 because it is the only type specimen (SCHINDLER 2015).

4.3 The cichlasomine bar pattern

The basic cichlasomine pattern of dark vertical bars is modified in the genus *Heros* in several ways (cf. KULLANDER & SILFVERGRIP 1991, see ŘÍČAN et al. 2005 for development of bar pattern during ontogenesis). In adult *Heros* specimens bar 1 (on caudal fin base; caudal spot sensu KULLANDER 1983 and bar 1p [posterior part of bar 1] sensu ŘÍČAN et al. 2005) and bar 2 (sensu KULLANDER & SILFVERGRIP 1991, caudal peduncle bar 1a [anterior part of bar 1] sensu ŘÍČAN et al. 2005) located on the rear end of the caudal peduncle are usually fused. The only exception is *Heros liberifer*.

Bar 3 (bar 2 sensu ŘÍČAN et al. 2005) between the posterior rays of dorsal and anal fin extends partially to the dorsal fin (forming the dorsal fin spot sensu KULLANDER 1986) and is always very prominent. Bar 4 (bar 3 sensu ŘÍČAN et al. 2005) undergoes several modifications during the ontogenesis. This results in certain variations of its shape in adult specimens. In *H. liberifer* bar 4 is usually extending to the dorsal fin base, but in *H. severus* it is short and usually reaches only to the lower or at most below the upper lateral line. Bar 5 (bar 4 sensu ŘÍČAN et al. 2005) is always divided into an anterior and a posterior part in adult *Heros* for it splits during the ontogenesis. Bar 8 (bar 7 sensu ŘÍČAN et al. 2005) extending between the opercular cleft and the pectoral fin usually merges with the predorsal bar (predorsal spot sensu KULLANDER 1983, bar 8 sensu ŘÍČAN et al. 2005). As bar 8 and the predorsal bar are dorsally often not united in *H. liberifer*, both frequently appear as a wide Y-shaped bar.

In spite of the specific increase or decrease of the number of vertical bars caused by their fusion or division during the ontogenesis, adult *Heros* species usually have eight bars between their eye and their caudal fin. *Heros liberifer*,

however, has 9 bars, for bar 1 (caudal spot) is separated from bar 2 (see figs 1-5).

Although individual modifications occur (SCHINDLER 2015), our examination of numerous specimens of different *Heros* species in the field revealed that the specific pattern of dark vertical bars of different populations is stable (see STAWIKOWSKI & WERNER 1998, STAECK 2009). Consequently, it is a reliable means to delimitate species. Although the distinct appearance of the bars depends on the mood of the fish, the different shape of bar 4 in *Heros severus* and *H. liberifer* proved to be the most reliable means to distinguish between both in the field (see fig. 6).

4.4. Zoogeography

Heros severus and *H. liberifer* belong to the partially vicariant fish faunas of the two separate biogeographic provinces of the upper Rio Negro (a subbasin of the Amazon) and the upper Rio Orinoco (GÉRY 1969, HUBERT & RENNO 2006, WINEMILLER et al. 2008, WINEMILLER & WILLIS 2011). The type locality of *Heros severus* is in the vicinity of the town of Marabitanas in the drainage of the upper Rio Negro. Additional collecting sites are known at São Gabriel da Cachoeira and in the lower Rio Uaupés (RÖMER 1998, WARZEL 2003). Recently the occurrence of this species was also documented for several tributaries of the upper Rio Orinoco (STAECK 2009, RIETSCH in DITTRICH 2014). *Heros liberifer* has the center of its distribution in drainages of the middle and upper Rio Orinoco and up to now has not been reported from the Rio Negro basin.

The first to document the syntopic occurrence of *Heros severus* and *H. liberifer* in Venezuela was the first author (STAECK 2009). The syntopic distribution of both species in the Rio Casiquiare and the Rio Atabapo was later confirmed by RIETSCH (in DITTRICH 2014).

The Rio Casiquiare is a major waterway of the region. It functions as a dispersal corridor for fishes of the Rio Orinoco and Rio Negro (Amazon) basins, because it connects the upper Rio Orinoco and upper Rio Negro river systems

by taking one eighth to one quarter of the upper Orinoco main channel volume (STERNBERG 1975). WINEMILLER & WILLIS (2011) arrive at the conclusion that the degree to which the Rio Casiquiare serves as a dispersal corridor or barrier is variable and depends on the physiological and ecological tolerances of individual species. The effectiveness of its function as a free dispersal corridor is limited by the strong physicochemical and ecological gradient that spans its length (clear to white waters near its origin at the Orinoco bifurcation, black waters within its lower reaches at its junction with the upper Rio Negro). Thus, the Rio Casiquiare is a zoogeographic filter that permits only those species capable of dealing, either physiologically or ecologically, with a wide range of environmental conditions to disperse across this waterway and invade new river basin. For other species with narrow habitat requirements and consequently without such a tolerance, the Rio Casiquiare constitutes an ecological barrier for dispersal.

Although *Heros severus* and *H. liberifer* have a partially syntopic distribution, it appears that both have different physicochemical requirements. *Heros liberifer* is adapted to a wide range of environmental conditions and water types, for we found this species not only in clearwater and extreme blackwater conditions, but also in whitewater habitats (drainage of the lower Rio Manapiare: pH 6.1). Up to now, no collecting sites have been recorded from the drainage of the Rio Negro. This, however, is probably due to the fact that this region is only poorly sampled. As *H. liberifer* occurs in the lower Rio Casiquiare close to its mouth (STAECK 2009), it is highly probable that it is also distributed in the drainage of the upper Rio Negro. If this hypothesis is confirmed, *H. liberifer* will belong to the fish species that could disperse across the Rio Casiquiare because of their wide physicochemical requirements.

In contrast, *H. severus* seems to be a blackwater adapted species with narrow habitat requirements. All our collecting sites of this species were exclusively extremely acidic blackwater habitats with very low pH and conductivity (pH 4.1-4.2). These observations suggest that

this cichlid is exclusively restricted to blackwater habitats. Thus, it appears that *H. severus* is one of the blackwater species which could not use the Rio Casquiare as a dispersal corridor. Instead it dispersed from the upper Rio Negro subbasin to the Rio Orinoco basin via alternative waterways, e. g. the blackwater connections between the upper Rio Negro and the Rio Atabapo in the vicinity of the Isthmus of Pimichin between the towns of Maroa and San Antonio de Yavita (WINEMILLER & WILLIS 2011).

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