

## Taxonomic study of *Hoplias microlepis* (Günther, 1864), a trans-Andean species of trahiras (Ostariophysi: Characiformes: Erythrinidae)

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The *Hoplias malabaricus* species group represents one of the most complex taxonomical problems in the systematics of Neotropical fishes, including specimens widely distributed in most drainages of South America and part of Central America with great variation or overlap of putative diagnostic characters. The large number of nominal species, many of which without known type material, renders the problem more complicated. Currently, at least three nominal species can be included in the *Hoplias malabaricus* species group based on the form of the medial margins of dentaries and presence of tooth plates on the tongue: *Hoplias malabaricus*, *H. teres*, and *H. microlepis*, the latter representing the only exclusively trans-Andean known species of the genus. We present herein a taxonomic study of *Hoplias microlepis* based on examination of syntypes and recently collected specimens, including a redescription of the species. *Hoplias microlepis* occurs in the Pacific drainages of Panama and Southwestern Costa Rica, in addition to the río Guayas basin in Ecuador and the region near its mouth (río Tumbes, Northwestern Peru). Records of the species on the Atlantic coast of Panama are restricted to the Canal Zone, suggesting dispersal through the Panama Canal. We also designate lectotype and paralectotypes.

O grupo de espécies *Hoplias malabaricus* representa um dos problemas taxonômicos mais complexos na sistemática de peixes Neotropicals, com ampla distribuição em quase todas as bacias da América do Sul e parte da América Central e grande variação ou sobreposição de prováveis caracteres diagnósticos. O grande número de espécies nominais, muitas delas sem material-tipo conhecido, é um fator complicador nessa questão. Atualmente, pelo menos três espécies nominais podem ser incluídas no grupo de espécies *Hoplias malabaricus*, com base no formato das margens mediais dos dentários e presença de dentes na língua: *Hoplias malabaricus*, *H. teres* e *H. microlepis*, a última sendo a única espécie exclusivamente trans-andina do gênero conhecida até o momento. Apresentamos aqui um estudo taxonômico de *Hoplias microlepis*, com exame dos síntipos e exemplares coletados mais recentemente, incluindo uma redescrição da espécie. *Hoplias microlepis* distribui-se nas bacias da costa Pacífica do Panamá e sudoeste da Costa Rica, além da bacia do río Guayas no Equador e região próxima à sua foz (río Tumbes, noroeste do Peru). Registros da espécie na costa Atlântica do Panamá são restritos à Zona do Canal, sugerindo dispersão através do Canal do Panamá. São designados também lectótipo e paralectótipos.

**Key words:** Central America, *Hoplias malabaricus* species group, Taxonomy, Trans-Andean distribution, Wolf fish.

### Introduction

The Erythrinidae is a Neotropical characiform family comprising three extant genera, *Erythrinus* Scopoli, *Hoplerhythrinus* Gill, and *Hoplias* Gill, the latter constituting the most speciose of the three (Oyakawa, 2003). Oyakawa (1990) and Oyakawa & Mattox (2009) defined three groups within *Hoplias*: the *H. macrophthalmus* group which comprises a single valid species, *H. aimara* (Valenciennes)

(see Mattox *et al.*, 2006), the *H. lacerdae* group currently including five valid species (*H. australis* Oyakawa & Mattox, *H. brasiliensis* (Spix), *H. curupira* Oyakawa & Mattox, *H. intermedius* (Günther) and *H. lacerdae* Miranda-Ribeiro, see Oyakawa & Mattox, 2009) and the *H. malabaricus* group, still lacking a proper taxonomic approach. Contrary to what was mentioned by Blanco *et al.* (2010), *H. aimara* is not included in the *H. lacerdae* group, but rather assigned to the *H. macrophthalmus* group (see Mattox *et al.*, 2006; Oyakawa

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& Mattox, 2009). This error has been repeated by subsequent authors (e.g., Blanco *et al.*, 2011; Cioffi *et al.*, 2012; Marques *et al.*, 2013). Similarly, *H. microlepis* (Günther) and *H. teres* (Valenciennes) were not included in the *H. lacerdae* group as stated by Marques *et al.* (2013), but rather belong to the *H. malabaricus* group (see below).

*Hoplias malabaricus* (Bloch) represents perhaps one of the most complex problems in the taxonomy of Neotropical fishes. This species is widespread in South America (e.g., Géry, 1977) occurring in drainages of both sides of the Andes. Meristic and morphometric data of specimens greatly overlap throughout the distribution range of the species (e.g., Bifi, 2013), and there is a large number of nominal species currently considered junior synonyms (e.g., Oyakawa, 2003), many of which without known type material. In addition, numerous cytogenetic studies have suggested that *H. malabaricus* represents a species complex (e.g., Bertollo *et al.*, 1986; Dergam & Bertollo, 1990; Bertollo *et al.*, 1997; 2000; Born & Bertollo, 2001; 2006; Cioffi *et al.*, 2009a, 2009b; Rosa *et al.*, 2009; Santos *et al.*, 2009; Blanco *et al.*, 2010; 2011; Cioffi & Bertollo, 2010; Cioffi *et al.*, 2011a, 2011b, 2011c, 2011d, in press; Marques *et al.*, 2013).

The *Hoplias malabaricus* species group was defined by Oyakawa (1990) and Oyakawa & Mattox (2009) to include species with the dentaries abruptly converging towards the mandibular symphysis and with tooth plates on the tongue. Based on these characters, at least two nominal species of *Hoplias* can be assigned to the group in addition to *H. malabaricus*: *H. microlepis*, and *H. teres*, the former having a trans-Andean distribution and the latter known from Lago Maracaibo, Venezuela. As an initial attempt to address the taxonomic complexity of the *H. malabaricus* species group, in the present study we present a redescription of *H. microlepis*, designate lectotype and paralectotypes, and estimate the geographic distribution of the species.

### Material and Methods

This study was based on meristic and morphometric data from 64 specimens, including seven syntypes. Meristic data were taken under a stereomicroscope and the morphometric data were taken point-to-point with a digital caliper to 0.1 mm. Measurements and counts were made on the left side of the body, whenever possible, and follow Fink & Weitzman (1974) and Mattox *et al.* (2006). Unbranched and branched fin-ray counts are presented as Roman and Arabic numbers, respectively. Vertebral counts were made on radiographed specimens and include the anterior four vertebrae of the Weberian apparatus. The asterisk in the meristic characters refers to values of the lectotype. Osteological names follow Weitzman (1962) and Roberts (1969). Descriptions of coloration were based on specimens preserved in ethanol. Institutional abbreviations follow Ferraris Jr. (2007).

## Results

### *Hoplias microlepis* (Günther, 1864)

#### Figs. 1-3

*Macrodon microlepis* Günther, 1864: 282 [original description; type-locality: Western Ecuador and Chagres River]. -Eigenmann & Eigenmann, 1889: 102 [diagnosis in key, citation to Western slopes of South America from Guayaquil to Panama].

*Macrodon trahira* var. *microlepis* Steindachner, 1880: 101 [citation to Guayaquil, Ecuador].

*Hoplias microlepis*. -Starks, 1906: 772 [comparison with *Hoplias malabaricus*, citation to Guayaquil, Ecuador]. -Regan, 1908: 167 [redescription, citation to Rio Chagres, Panama and Western Ecuador]. -Meek & Hildebrand, 1916: 303 [diagnosis in key, citation to both slopes of Panama and the Western slope of Ecuador]. -Eigenmann, 1921: 508-511 [citation, distribution]. -Eigenmann, 1922: 169 [diagnosis in key, citation to Pacific slope of Southern Ecuador and both slopes of Central Panama]. -Hildebrand, 1938: 290 [distribution]. -Bussing, 1966: 218 [citation to Puntarenas, Costa Rica]. -Géry, 1977: 102 [diagnosis in key, citation to Pacific slope of Southern Ecuador, Panama and Costa Rica]. -Ortega & Vari, 1986: 10 [checklist, citation to Peru]. -Oyakawa, 2003: 240 [checklist, distribution]. -Barriga, 1991: 31 [checklist]. -Ortega *et al.*, 2011: 39 [checklist, citation to Peru]. -Barriga, 2012a: 110 [distribution, endemism in Guayas basin]. -Barriga, 2012b: 213 [citation to Ecuador with photograph]. -Aguirre *et al.*, 2013 [morphological and genetic divergence among populations in Ecuador].

**Lectotype. Panama. Panama Province.** Chagres basin: BMNH 1864.1.26.221, 269.7 mm SL, Chagres River, purchased of Mr. Salvin (Fig. 1) [designated herein].

**Paralectotypes. Ecuador.** BMNH.1860.6.16.128, 1, 276.6 mm SL, West Ecuador, collector Fraser; BMNH.1860.6.16.154-155, 3, 96.6-118.5 mm SL, West Ecuador, collector Fraser; **Panama. Panama Province.** Chagres basin: BMNH 1864.1.26. 222, 1, 222.8 mm SL, same information as lectotype; BMNH 1864.1.26.309, 1, 175.6 mm SL, same locality as lectotype, collected by Messrs. Dow & Salvins (Fig. 2). [all designated herein].

**Material examined. Ecuador. Guayas.** Río Daule basin: BMNH 1898.11.4.45, 1, 230.9 mm SL, río Daule, West Ecuador, Dr. H. Festa; BMNH 1920.12.20.129-130, 2, 207.9-254.1 mm SL, Colimes, C. H. Eigenmann; BMNH 1920.12.30.131-132, 2, 174.1-188.9 mm SL, Guayaquil, C. H. Eigenmann; FMNH 93480, 5, 60.5-126.3 mm SL (5 specimens radiographed), Los Ríos, Río Palenque, Estación Biológica Río Palenque, about 5 miles downstream from station in an isolated pool, G. S. Glodek, G. Whitmire & J. Dryan, 30 Jul 1974; USNM 53512, 2, 217.5-219.5 mm SL, Guayaquil, P. Simmons; USNM 94064, 6, 234.6-296.4 mm SL, Guayaquil, W. L. Schmitt, 05 Jan 1934; **Panama. Chiriquí.** USNM 78601, 1, 252.8 mm SL, Bas Obispo, Mandingo River, S. E. Meek & S. F. Hildebrand, 02 Feb 1911; **Coclé.** USNM 310650, 1, 85.3 mm SL, Membrillal River at bridge on IAH (Inter-American Highway), about 5 miles East of Divisa, H. Loftin *et al.*, 25 Feb 1962; USNM 310676, 1, 140.7 mm SL, creek about 3 miles West of Hato River at bridge on IAH (Inter-American Highway), H. Loftin & E. Tyson, 14 Oct 1961; **Colón.** USNM 78606, 2, 131.2-141.5 mm SL, small creek at

Mindi, S. E. Meek & S. F. Hildebrand, 21 Jan 1911; USNM 78608, 10, 55.7-108.9 mm SL, Gatún River, Canal Zone, S. E. Meek & S. F. Hildebrand, 24 Jan 1911; USNM 78609, 4, 128.3-182.3 mm SL (4 specimens radiographed), creek opposite Mindi Cut, S. E. Meek & S. F. Hildebrand, 17 Jan 1911; USNM 78613, 2, 143.2-156.9 mm SL (2 specimens radiographed), Mindi creek, French Cut-Off, Canal Zone, S. E. Meek & S. F. Hildebrand, 2 Mar 1911; USNM 78614, 4, 106.5-137.9 mm SL, Gatún River, Monte Lirio, Canal Zone, S. E. Meek & S. F. Hildebrand, 27 Mar 1911; USNM 78615, 4, 143.2-156.9 mm SL (4 specimens radiographed), Largateria Creek, Canal Zone, S. E. Meek & S. F. Hildebrand, 09 Mar 1911; USNM 78617, 11, 143.2-156.9 mm SL (9 specimens radiographed), Mindi Creek, Canal Zone, S. E. Meek & S. F. Hildebrand, 14 Jan 1911; USNM 310672, 1, 79.6 mm SL, Agua Salud creek on pipeline road near Gamboa, H. Loftin, *et al.*, 31 Dec 1961; **Darién**. USNM 293250, 5, 164.7-176.2 mm SL (5 specimens radiographed), Pirre River, Tuira, above El Real, 8°05'60"N 77°45'00"W, J. Lundberg, B. Chernoff & L. Mcdade, 16 Feb 1985; **Herrera**. USNM 310444, 1, 186.7 mm SL (1 specimen radiographed), Barrera near Pesé, H. Loftin & E. Tyson, 1961; USNM 310678, 1, 130.4 mm SL, Herrera Creek about 4 miles up Pesé road from junction with Chitre-Divisa Road, H. Loftin & E. Tyson, 21 Oct 1961; **Los Santos**. USNM 78595, 3, 131.1-163.7 mm SL, río Abajo, S. E. Meek & S. F. Hildebrand, 22 Apr 1911; **Panama Province**. USNM 78603, 2, 37.8-186.3 mm SL (2 specimens radiographed), Juan Diaz River, S. E. Meek & S. F. Hildebrand, 17 Jul 1911; USNM 78605, 11, 37.8-186.3 mm SL (6 specimens radiographed), Alhajuella, Limon Creek, S. E. Meek & S. F. Hildebrand, 26 Feb 1911; USNM 78607, 1, 138.1 mm SL, río Chagres, Gorgona, S. E. Meek & S. F. Hildebrand, 01 Apr 1912; USNM 109278, 3, 35.4-153.4 mm SL, small creek tributary to Chagres River, Madden Dam Road, S. E. Hildebrand, 14 Feb 1935; USNM 310673, 1, 129.9 mm SL, creek at bridge on IAH (Inter-American Highway), about 4 miles East of Pacora X-Road, G. H. Loftin & M. Smith, 24 Apr 1962; **Veraguas**. MZUSP 47931, 2, 45.3-106.0 mm SL, creek at bridge about 9 miles from Santiago on San Francisco Road, H. G. Loftin, 14 Jan 1962; MZUSP 47932, 1, 132.7 mm SL, río Frijoles, S. E. Meek & S. F. Hildebrand, 14 Mar 1911; USNM 78597, 1, 151.6 mm SL, Trinidad River, Icc. Hydro Station, S. E. Meek & S. F. Hildebrand, 08 Mar 1911; USNM 78598, 2, 134.4-138.7 mm SL, Gatun, Trinidad River, S. E. Meek & S. F. Hildebrand, 24 Jan 1911; USNM 78599, 2, 116.1-144.7 mm SL, Agua Clara, Trinidad River, S. E. Meek & S. F. Hildebrand, 10 Mar 1911; USNM 78600, 1, 148.5 mm SL, Agua Clara, Trinidad River, Canal Zone, S. E. Meek & S. F. Hildebrand, 10 Mar 1911; USNM 78611, 5, 32.3-138.2 mm SL, Frijoles River, Canal Zone, S. E. Meek & S.

F. Hildebrand, 13 Feb 1911; USNM 78612, 1, 98.5 mm SL, Gorgona Reservoir, Canal Zone, S. E. Meek & S. F. Hildebrand, 28 Mar 1912; USNM 310677, 1, 70.2 mm SL, creek 13 miles West of Ocu X-road, Loftin, *et al.*, 21 Oct 1961; USNM 310680, 1, 189.4 mm SL, creek 20 miles West of Santiago, H. Loftin, 1961.

**Diagnosis.** *Hoplias microlepis* differs from all other species of *Hoplias*, except for species of *H. malabaricus* group, in the shape of the dentaries abruptly converging towards the mandibular symphysis (Oyakawa & Mattox, 2009: 118, Fig. 1d) (*vs.* dentaries parallel and only gently converging towards the mandibular symphysis) and by the presence of tooth plates on tongue (*vs.* tooth plates on tongue absent). *H. microlepis* is also distinguished from *H. brasiliensis* and *H. curupira* in the number of scales along lateral line (43-47 *vs.* 38-43 and 34-39, respectively), and from *H. australis* and *H. lacerdae* in the number of pores of the laterosensory system along the ventral surface of dentary (4 *vs.* always 5 and 6-8 respectively). *H. microlepis* is distinguished from *H. aimara* by the presence of the accessory ectopterygoid and lack of a vertically elongate dark spot on the opercular membrane (*vs.* accessory ectopterygoid absent and dark spot present). *H. microlepis* is distinguished from the other species in the *H. malabaricus* species group by the higher number of scales around the caudal peduncle (22-24, usually 24 *vs.* 18-20, usually 20).

**Description.** Morphometric data presented in Table 1. Body cylindrical, deeper than wide. Greatest body depth at vertical through fifth or sixth scale anterior to dorsal-fin origin in specimens smaller than 61.4 mm SL, closer to dorsal-fin origin in larger specimens. Anterior profile of head angular in lateral view. Overall dorsal profile of head straight, slightly convex anteriorly towards snout. Dorsal margin of orbit located at horizontal through dorsal profile of head in specimens smaller than 45.3 mm SL, but not reaching dorsal profile of head in larger specimens (*ca.* 61.4 mm SL). Dorsal profile of trunk slightly convex from vertical through first series of scales of body to dorsal-fin origin; straight and



**Fig. 1.** *Hoplias microlepis* (lectotype of *Macrodon microlepis*), BMNH 1864.1.26.221, 269.7 mm SL, Chagres River, Panama.



**Fig. 2.** *Hoplias microlepis* (paralectotypes of *Macrodon microlepis*). (a) BMNH 1864.1.26.222, 222.8 mm SL, Chagres River, Panama; (b) BMNH 1864.1.26.309, 175.6 mm SL, Chagres River, Panama; (c) BMNH 1860.6.16.128, 276.6 mm SL, West Ecuador; (d) BMNH 1860.6.16.154-155, 96.6 mm SL, West Ecuador; (e) BMNH 1860.6.16.154-155, 108.2 mm SL, West Ecuador; (f) BMNH 1860.6.16.154-155, 118.5 mm SL, West Ecuador.

posteroventrally inclined along dorsal-fin base; straight and less inclined to slightly concave from vertical through base of last dorsal-fin ray to origin of anteriormost dorsal procurent caudal-fin ray. Ventral profile of lower jaw distinctly angular in region of mandibular symphysis, straight to slightly inclined from vertical through anterior nostril to posterior margin of lower jaw. Medial margins of contralateral dentaries abruptly converging anteriorly towards symphysis. Ventral profile of trunk slightly convex to pelvic-fin origin; approximately straight to slightly convex from latter point to anal-fin origin; straight and posterodorsally inclined along anal-fin base; straight or slightly concave from base of last anal-fin ray to anteriormost ventral procurent caudal-fin ray.

Upper jaw slightly shorter than lower jaw. Posterior portion of maxilla dorsally enlarged and extending medially to anterior margins of second and third infraorbitals. Upper and lower lips fleshy, with short projections of skin covering canines externally. Anterior nostril tubular with anterior slit reaching base of tubular portion. Anterior and posterior nostrils situated along horizontal through center of orbit, posterior nostril situated midway between anterior nostril and anterior margin of orbit. Eye proportionately larger in smaller specimens. Infraorbital bones well developed and horizontally elongate. Infraorbitals 3, 4, and ventral portion of 5 partially covering preopercle. Anteroventral margin of infraorbital 3 relatively straight and posteroventral margin convex. Posterior margin of infraorbitals 4, 5, and 6 slightly convex.

Teeth in both jaws conical or canine. Premaxillary teeth in single row. First premaxillary tooth large canine, second tooth medium sized canines. Seventh tooth canine almost as large as

anterior most premaxillary canine. Third to sixth, and eighth premaxillary teeth small and conical. Maxilla with single row of approximately 38-39 relatively small teeth, except for very well-developed canine-like fourth or fifth tooth. Dentary with anterior external row of teeth and posterior internal row. External series with four anterior small teeth, followed by two well-developed canines with posterior canine larger than anterior canine, and then 11 conical teeth slightly smaller than anterior most dentary canine. Internal series beginning immediately posterior to last conical tooth of external row and composed of approximately 15 very small teeth. Accessory ectopterygoid and ectopterygoid toothed. Ectopterygoid with series of small conical teeth along ventrolateral margin and many smaller viliform teeth on ventromedial surface. Endopterygoid edentulous.

Distal margins of all fins rounded. Dorsal-fin rays ii, 11-13 (mode: ii,12\*, n = 64). Dorsal fin located at midbody, its origin at vertical through approximately fourth scale anterior to series along pelvic-fin origin. Longest dorsal-fin ray approximately three-quarters of body depth. Anal-fin base short. Anal-fin rays ii-iii, 7-9 (mode: ii,8\*, n = 61). Tip of depressed dorsal fin reaching vertical through anal-fin origin in small specimens (less than 138 mm SL) but falling short of that point in larger specimens. Pectoral-fin rays i,10-14 (mode: i,13, n = 63, lectotype with i,12). Pectoral-fin origin located at about vertical through median region of opercle. Tip of pectoral fin separated from pelvic-fin origin by three to five scales. Pectoral and pelvic fins of similar size. Pelvic-fin rays i,7\* (n = 64). Pelvic-fin origin situated at midbody and approximately four scales posterior to vertical through dorsal-fin origin. Tip of pelvic fin separated from anal-fin origin by five or six scales. Caudal-fin rays i,15,i\* (n =58).

**Table 1.** Morphometric data of *Hoplias microlepis*. Standard length in mm; values 1-14 are percentages of the standard length and values 15-22 are percentages of head length. n = number of examined specimens, SD = standard deviation.

|                            | Lectotype | Paralectotypes |      |            |     | Non-type material |      |            |     |
|----------------------------|-----------|----------------|------|------------|-----|-------------------|------|------------|-----|
|                            |           | n              | Mean | Range      | SD  | n                 | Mean | Range      | SD  |
| Standard length            | 269.7     | 6              | -    | 96.6-276.6 | -   | 57                | -    | 35.4-296.4 | -   |
| 1. Body depth              | 20.5      | 6              | 22.2 | 20.0-28.4  | 3.4 | 54                | 22.1 | 15.9-26.5  | 2.3 |
| 2. Head length             | 30.2      | 6              | 33.1 | 29.8-36.1  | 2.7 | 57                | 31.8 | 29.0-36.7  | 1.5 |
| 3. Pectoral-fin length     | 17.1      | 6              | 18.0 | 16.9-19.7  | 0.9 | 56                | 18.1 | 15.7-20.2  | 0.9 |
| 4. Pelvic-fin length       | 18.3      | 6              | 20.1 | 18.4-21.6  | 1.5 | 57                | 19.7 | 17.8-21.8  | 0.9 |
| 5. Anal-fin length         | 18.0      | 3              | 18.8 | 18.0-19.3  | 0.7 | 57                | 19.3 | 16.8-22.8  | 1.1 |
| 6. Dorsal-fin length       | 31.5      | 6              | 31.7 | 29.8-34.1  | 1.6 | 56                | 30.8 | 28.1-34.2  | 1.3 |
| 7. Dorsal-fin base         | 20.2      | 6              | 19.5 | 18.6-20.7  | 0.8 | 57                | 18.5 | 16.5-20.1  | 0.8 |
| 8. Anal-fin base           | 9.1       | 3              | 9.7  | 9.5-10.0   | 0.2 | 57                | 9.8  | 8.0-11.8   | 0.7 |
| 9. Pre-pectoral distance   | 28.3      | 6              | 30.5 | 27.0-33.3  | 2.4 | 57                | 29.1 | 26.1-37.1  | 1.7 |
| 10. Pre-pelvic distance    | 53.0      | 6              | 54.3 | 50.2-56.8  | 2.6 | 55                | 54.8 | 50.5-58.7  | 1.9 |
| 11. Pre-dorsal distance    | 48.1      | 6              | 52.5 | 47.3-56.1  | 3.4 | 57                | 50.5 | 46.2-57.8  | 2.1 |
| 12. Pre-anal distance      | 79.7      | 5              | 82.9 | 75.8-85.9  | 4.1 | 57                | 81.2 | 77.0-84.7  | 1.8 |
| 13. Caudal-peduncle depth  | 12.6      | 6              | 13.8 | 12.2-15.5  | 1.2 | 57                | 13.6 | 11.5-15.8  | 0.9 |
| 14. Caudal-peduncle length | 15.2      | 3              | 14.7 | 14.3-15.4  | 0.6 | 17                | 14.5 | 12.4-16.0  | 1.0 |
| 15. Head depth             | 45.2      | 6              | 45.2 | 41.8-48.4  | 2.5 | 57                | 50.7 | 43.2-57.3  | 3.4 |
| 16. Snout length           | 24.7      | 6              | 25.4 | 24.6-26.0  | 0.5 | 57                | 24.7 | 21.5-26.8  | 1.0 |
| 17. Snout width            | 25.0      | 6              | 22.5 | 20.0-26.5  | 2.4 | 57                | 23.0 | 18.4-26.1  | 1.4 |
| 18. Snout depth            | -         | -              | -    | -          | -   | 40                | 26.0 | 22.9-29.2  | 1.6 |
| 19. Pre-nasal distance     | 16.3      | 6              | 14.6 | 11.7-16.1  | 1.5 | 56                | 15.7 | 13.4-22.9  | 1.6 |
| 20. Orbital diameter       | 15.1      | 6              | 16.1 | 12.9-17.6  | 1.7 | 57                | 18.5 | 14.1-27.6  | 2.4 |
| 21. Interorbital width     | 29.1      | 6              | 25.9 | 23.8-28.2  | 1.8 | 57                | 26.1 | 21.6-30.1  | 1.8 |
| 22. Upper jaw length       | 54.8      | 6              | 49.4 | 47.5-51.1  | 1.5 | 57                | 51.6 | 48.3-56.6  | 1.5 |

Well-developed cycloid scales imbricated along body. Series of dorsal scales beginning at vertical on posterior margin of parietals and overlapping supraoccipital spine. Last vertical series of scales on caudal peduncle forming straight vertical line on caudal-fin base in lateral view. Anterior margin of scales with small concavity and posterior margin rounded. Approximately twelve *radii* extending from center of scale to its anterior margin and around sixteen *radii*, some anastomosed, extending from center of scale to its dorsal, posterior, and ventral margins. Lateral line straight and complete, extending from posteroventral margin of supracleithrum to posteriormost scale on body. Lateral line with 43-47 (mode: 45, n = 61, lectotype with 44) scales. Longitudinal series of scales between lateral line and dorsal-fin origin 6.5-7.5 (mode: 6.5\*, n = 63). Longitudinal series of scales between lateral line and pelvic-fin origin 5.5-6.5 (mode: 5.5\*, n = 63). Longitudinal series of scales around caudal peduncle 22-24 (mode: 24\*, n = 62).

Approximately 9 gill rakers on first epibranchial, most in form of small denticulated plates. Lower branch of first branchial arch with 4-6 (mode: 5\*, n = 48) more elongate rakers and approximately 10 plate-like rakers. Laterosensory canal along ventral surface of dentary with 4\* (n = 61) pores, one specimen with 5 pores. Total vertebrae: 42-45 (n = 41), 28-30 precaudal and 13-15 caudal vertebrae.

**Color in alcohol.** Ground coloration of head and body dark to light brown, darker dorsally and paler ventrally (Fig. 3). Ventral region homogeneously white or light yellow in specimens up to 106.2 mm SL. Larger specimens (*i.e.*, 130.0 mm SL) with scales of ventrolateral surface of body with white central portion bordered by darker pigmentation, giving aspect of thin longitudinal dark and pale stripes. Specimens up to 60 mm SL with conspicuous dark longitudinal stripe along lateral line scales, covering approximately half of the series immediately above and below lateral line. Longitudinal dark stripe less conspicuous in larger specimens. Approximately five to six darker parallel

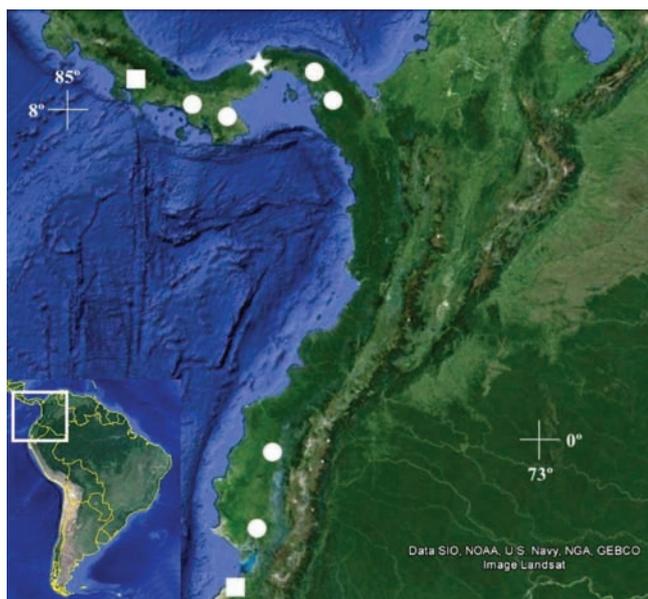
diagonal bars along dorsal region extending anteroventrally to just below lateral line (Fig. 3). Diagonal dark bars in many specimens continuing posteroventrally to approximately three longitudinal scale series below lateral line, resulting in chevron-like pattern. Dorsal portions of bars more evident than ventral portions. Bars more conspicuous in specimens with light brown ground coloration. Specimens larger than 106.0 mm SL with conspicuous round spot on dorsal portion of caudal peduncle, near base of uppermost caudal-fin rays (Fig. 3). Dorsal surface of head dark brown. Lips with alternating dark and light vertical bands, inconspicuous in some specimens. Ventral surface of dentaries varying from white in small specimens (*ca.* 35.4 mm SL), to alternating dark and light transverse stripes in specimens larger than 61.4 mm SL. Coloration of infraorbital region and dorsal surface of head similar to each other. Many specimens with two dark stripes radiating posteriorly from eye along infraorbital 6 and dorsal portion of infraorbital 3. Ground coloration of opercular series dark brown. Opercular membrane usually lighter than opercle (Fig. 3).

All fins light brown, lighter than body in some specimens, with dark spots on rays and interradial membranes forming pattern of irregular dark stripes (Figs. 1, 2a-b, 3). Stripes on pelvic, anal and caudal fins wider and more regular than those on dorsal fin. Ventral surfaces of pectoral and pelvic fins either lighter than, or with same pattern as, dorsal surface, but with pattern less conspicuous. Fins of largest specimens (*ca.* 163.0 mm SL) usually darker than rest of body.

**Distribution.** *Hoplias microlepis* occurs in rivers along the entire Pacific coast of Panama and in rivers tributaries to the Panama Canal including the Atlantic coast. The species also occurs in the río Guayas basin which empties in the Gulf of Guayaquil, Ecuador. Although we did not examine specimens from Costa Rica and Peru, there are records in the literature of *Hoplias microlepis* in Puntarenas, Southwestern Costa Rica (Bussing, 1966) and río Tumbes, Northwestern Peru (Ortega & Vari, 1986) (Fig. 4).



**Fig. 3.** *Hoplias microlepis*, USNM 293250, 176.2 mm SL, Pirre River, Tuira, Panama.



**Fig. 4.** Map of Northwestern South America and part of Central America showing geographic distribution of *Hoplias microlepis* based on material examined herein (star and dots) and records from literature (squares). Star indicates type-locality at Chagres River, Panama. Some symbols may represent more than one lot.

### Discussion

The *Hoplias malabaricus* species group was defined by Oyakawa (1990) and Oyakawa & Mattox (2009) to include specimens with dentaries abruptly converging towards the mandibular symphysis and with bony tooth plates on the basihyal (*i.e.*, rough tongue). Examination of all syntypes of *H. microlepis* showed that they also have the dentaries abruptly converging towards the mandibular symphysis and a rough tongue. Hence, *H. microlepis* clearly belongs to the *H. malabaricus* species group. Syntypes of a third nominal species, *H. teres* from Lago Maracaibo, Venezuela, also have the dentaries abruptly converging towards the mandibular symphysis (M. Toledo-Piza, pers. com.). Although we do not have the information whether *H. teres* has bony tooth plates on the basihyal, the form of the dentaries in this species is typical of that of the *H. malabaricus* species group, a condition clearly different from the parallel dentaries present in all remaining species of *Hoplias* (*i.e.*, *H. lacerdae* species group and *H. aimara*) as well as in the other two genera of the Erythrinidae (*i.e.*, *Erythrinus* and *Hoplerythrinus*). More studies are needed, however, to clarify the identity of *H. teres* within the *H. malabaricus* species group and to find putative diagnostic characters for the species.

Günther (1864) described *Macrodon microlepis* based on seven specimens, three from “Chagres River” and four from “West Ecuador”, all deposited in the Natural History Museum,

London. As a diagnostic feature, Günther (1864) mentioned the presence of 11 scales around the dorsal margin of the caudal peduncle between contralateral lateral lines. Günther (1864) did not make reference to any of the seven specimens being the holotype of *M. microlepis*, and thus all of them are syntypes of the species. Following the article 74 of the International Code of Zoological Nomenclature (ICZN, 1999), we herein designate one of the specimens as the lectotype (BMNH 1864.1.26.221) (Fig. 1), and the remaining six specimens are designated as paralectotypes (BMNH.1860.6.16.128, BMNH.1860.6.16.154-155, BMNH 1864.1.26.222, BMNH 1864.1.26.309) (Fig. 2). Oyakawa (2003:240) cited three lots of syntypes of *H. microlepis*, but examination of all syntypes deposited at the Natural History Museum, London, revealed that two of the numbers cited by Oyakawa (2003) (BMNH 1860.6.16.154-55 and BMNH 1860.6.18.21-22) were at the same jar with three specimens. Apparently an error occurred when this lot was catalogued, and as a curatorial procedure to amend this, it was chosen the number BMNH 1860.6.16.154-55 for this lot, with the other number (BMNH 1860.18.21-22) unutilized (J. MacLaine, pers. com.). In addition, we also list three additional lots of syntypes not mentioned by Oyakawa (2003) and corrected the number of specimens of each lot.

Steindachner (1874; 1880) mentioned two species of *Macrodon* in Central America: *M. trahira* and *M. microlepis*, the latter considered a subspecies of *M. trahira* in his 1880 publication. He listed the same diagnostic character for *M. microlepis* as proposed by Günther (1864) (*i.e.*, the relatively high number of scales around the dorsal portion of the caudal peduncle between lateral lines) emphasizing that this was the only difference he could find between both forms (Steindachner, 1880:49). Eigenmann & Eigenmann (1889) considered two valid species in *Macrodon*: *M. microlepis* with 11 series of scales between lateral lines on the dorsal portion of the caudal peduncle and 43-44 lateral line scales, and *M. malabaricus* with nine series of scales between lateral lines on the dorsal portion of the caudal peduncle and 39-43 lateral line scales. Although both characters might be useful in the identification of *H. microlepis* within the geographic distribution of the species, as mentioned by Eigenmann & Eigenmann (1889), we point out that the count of lateral-line scales in *Hoplias malabaricus* from other localities (*e.g.*, a few forms of *H. malabaricus* from the La Plata basin; Bifi, 2013) greatly overlaps that of *H. microlepis*, and its use should be done with caution. In addition, the number of lateral-line scales of *H. australis*, *H. intermedius*, and *H. lacerdae*, all from the *H. lacerdae* species group, also overlaps that of *H. microlepis* (Oyakawa & Mattox, 2009). The number of scales around the caudal peduncle, on the other hand, does not overlap between *H. microlepis* and *H. malabaricus* and hence constitutes the only meristic character truly diagnostic for *H. microlepis* among other species of *Hoplias*.

Gill (1903) proposed a new name, *Hoplias*, to include all erythrinids previously classified in *Macrodon*, since the latter genus was preoccupied in the Sciaenidae. Starks (1906) was the first author to use the new combination for *Hoplias microlepis*, an act followed by subsequent authors (*e.g.*, Regan, 1908, Meek & Hildebrand, 1916, Eigenmann, 1921).

Hubbs (1953) made a few taxonomic considerations regarding *Hoplias microlepis*. In the heading of the section concerning this species, he erroneously cited the year of publication as 1860 instead of 1864. Although Günther (1864) in the original description of *H. microlepis* mentioned the species as occurring in Guatemala, Hubbs (1953) correctly stated that this was in error since Günther (1864) only examined the syntypes from Western Ecuador and Chagres River, Panama. In addition, Hubbs (1953) selected Chagres River as the type locality of *H. microlepis*, probably due to the better condition of specimens from this locality among all seven syntypes (Figs. 1-2). However, as Hubbs (1953) did not designate a lectotype, his act is not valid and the type locality should encompass the localities of all syntypes together (Article 76 of ICZN, 1999). Nevertheless, among the syntypes, specimens from Chagres River are indeed the best ones in overall condition and we herein selected one of them as the lectotype, which establishes Chagres River, Panama as the type locality.

*Hoplias microlepis* has an intriguing disjoint distribution in trans-Andean South America, already mentioned by Eigenmann (1921: 507-508). It is so far known only from the Guayas drainage in Ecuador and its surroundings (*i.e.*, río Tumbes, Northwestern Peru) and from the Pacific coast of Panama and Southwestern Costa Rica, leaving a large gap along the entire coast of Colombia (Fig. 4). There are a few species of freshwater fishes occurring in the Pacific slope from Panama to Ecuador (*e.g.*, *Creagrutus affinis* Steindachner, *Roeboides occidentalis* Meek & Hildebrand, *Sciades dowii* (Gill)), a similar distribution to that of *H. microlepis*. However, all these species are also known from the Pacific slope of Colombia, a region where *H. microlepis* is apparently absent and substituted by *H. malabaricus* (*e.g.*, Eigenmann, 1921: 508). There is a relatively small number of lots of *Hoplias* from the Pacific slope of Colombia, but interestingly, all specimens from coastal rivers of this region previously identified as *H. microlepis* that we had access to actually belong to *Hoplias malabaricus* (*e.g.*, FMNH 50596, five specimens from río Pizarro; FMNH 56735, one specimen from río Raspadura; FMNH 56740, one specimen from río Magui). We cannot affirm that *H. microlepis* is indeed absent from the Colombian Pacific drainages, and further evidence regarding to whether the species is truly absent in the wide Pacific slope of Colombia or has just not been found yet depends on more collecting efforts in the area.

Recently, Aguirre *et al.* (2013) have conducted a study of *H. microlepis* in rivers and artificial impoundments along

the río Guayas drainage in Ecuador and concluded that there are significant genetic divergences between populations from rivers and impoundments, also suggesting some slight morphometric variation among these populations. In the context of the putative disjoint distribution of *H. microlepis* in rivers of Panama and Ecuador, it would be interesting to perform a genetic study between these populations to determine the level of molecular divergence among them, since our meristic and morphometric data greatly overlap in samples from these two countries. In addition, records of *H. microlepis* from the Atlantic slope of Panama are restricted to the Canal Zone and are contemporary to the construction of the Panama Canal in 1911-1912 (*e.g.*, Meek & Hildebrand, 1916: 305), suggesting a dispersion through the canal.

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