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LISTS OF SPECIES

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Fishes from the Tusubres River basin, Pacific coast, Costa Rica: checklist, identification key and photographic album

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Abstract: A checklist of the fishes of the Tusubres River basin, Pacific coast of Costa Rica, compiled from field and museum surveys is herein presented. A total of 54 species, representing 47 genera and 27 families, were recorded. Peripheral species were dominant (64.8%), followed by secondary freshwater fishes (20.4%); primary freshwater fishes accounted only for 14.8% of the total fish diversity. Eleotridae (6 spp.), Gobiidae (6 spp.), Poeciliidae (5 spp.) and Characidae (4 spp.) were the most diverse. Two species (*Caranx sexfasciatus*, Carangidae; and *Opisthonema libertate*, Clupeidae) were new records for Costa Rican freshwaters, and two species (*Gymnotus maculosus*, Gymnotidae; and *Lebiasina boruca*, Lebiasinidae) was found to have expanded ranges. An identification key and a complete photographic album of all fish species recorded in the basin are presented. The results of this investigation provide a framework for future studies on biogeography, ecology and conservation on fishes from this area.

Key words: Central America, ichthyofauna, inventory, new records

INTRODUCTION

The Tusubres River Basin (Figure 1), located on the Pacific slope of Costa Rica (09°47′–09°29′ N and 084°40′–084°18′ W), has a drainage area of 826 km² (Rojas 2011), which correspond to 1.6% of the total country area. Despite its small size, this basin has a relatively high diversity of fishes as a result of its environmental heterogeneity and geographic position (Alpírez 1985; Bussing 1998).

Biogeographically, the Tusubres River Basin is included within the Chiriquí-Santa María area of endemism (*sensu* Matamoros et al. 2014), and represents the northern limit of this area. The area is characterized by the presence of several South American lineages that dispersed north into Middle America, representing, in most cases, the northern limit of their distributions (Matamoros et al. 2014).

Traditionally, several authors (e.g., Bussing 1987, 1998; Angulo et al. 2013) have included the Tusubres River Basin within the Pirris River Basin. However, as noted by Rojas (2011), geographic, hydrological, climatic and ecological factors merit the recognition of the two basins as distinct units.

Despite its relatively high diversity and the risk of extirpation of some species due to human activities (mainly by deforestation, expansion of agricultural frontiers and intensive fishing; Bussing 1998; Rojas 2011), the fish fauna of this basin is relatively poorly known. Taking this in consideration, the aim of this study is to describe the composition and distribution of the ichthyofauna of the Tusubres River Basin as a framework for future studies of the biogeography, ecology and conservation of fishes from this area. A checklist, an identification key and a complete photographic album of the fish species are provided.

MATERIALS AND METHODS

A total of 19 sampling points were performed (Table 1; Figure 1). Fishes were collected using dip nets (30×40 cm

Table 1. Sampled localities in the Tusubres River basin, Pacific coast, Costa Rica (fish inventory).

N	Locality	Latitude (N)	Longitude (W)	Altitude (m)
1	Río Tulín, 0.5 km S of Tulín	09°45'20.67"	084°25'00.45"	455
2	Río Turrubaritos, Mataplatano	09°35'27.56"	084°31'54.84"	215
3	Río Tulín, 1.7 km S of Carmona	09°44'11.02"	084°27'32.03"	190
4	Río Turrubaritos, 6 km S of Bijagual	09°40'53.01"	084°33'00.19"	106
5	Río Tulín, 6.6 km NE of Montelimar	09°40'49.36"	084°28'59.45"	73
6	Quebrada el Descalzo, Gamalotillo, La Gloria de Puriscal	09°34'56.42"	084°27'01.44"	55
7	Río Tarcolitos, 1.4 km E of Tárcoles	09°45'23.21"	084°36'50.83"	37
8	Río Turrubaritos, 1.2 km NW of Montelimar	09°37'44.84"	084°31'15.07"	37
9	Quebrada Cañablancal, 1 km E of the Herradura Beach	09°39'20.00"	084°39'14.76"	33
10	Quebrada La Quina	09°35'42.79"	084°30'47.16"	20
11	Quebrada Subestación	09°35'35.63"	084°31'54.48"	20
12	Quebrada los Porras, Gamalotillo, La Gloria de Puriscal	09°37'59.77"	084°27'26.64"	20
13	Quebrada La Palma, Finca La Flor	09°32'07.03"	084°22'48.48"	17
14	Quebrada Visita, 4 km E of Esterillos	09°31'30.00"	084°25'04.00"	14
15	Río Tusubres, 300 m upstream from Jacó-Esterillos road	09°34'40.00"	084°31'54.01"	14
16	Río Tusubres, 1.8 km E of Quebrada Amarilla	09°34'11.80"	084°31'58.69"	13
17	Estero Tarcolitos, Tárcoles	09°45'28.80"	084°37'28.20"	12
18	Estero Aserradero, 3.5 km W of Esterillos	09°31'50.00"	084°29'19.68"	10
19	Estero Bejuco, Bejuco Beach	09°30'59.89"	084°25'18.40"	9

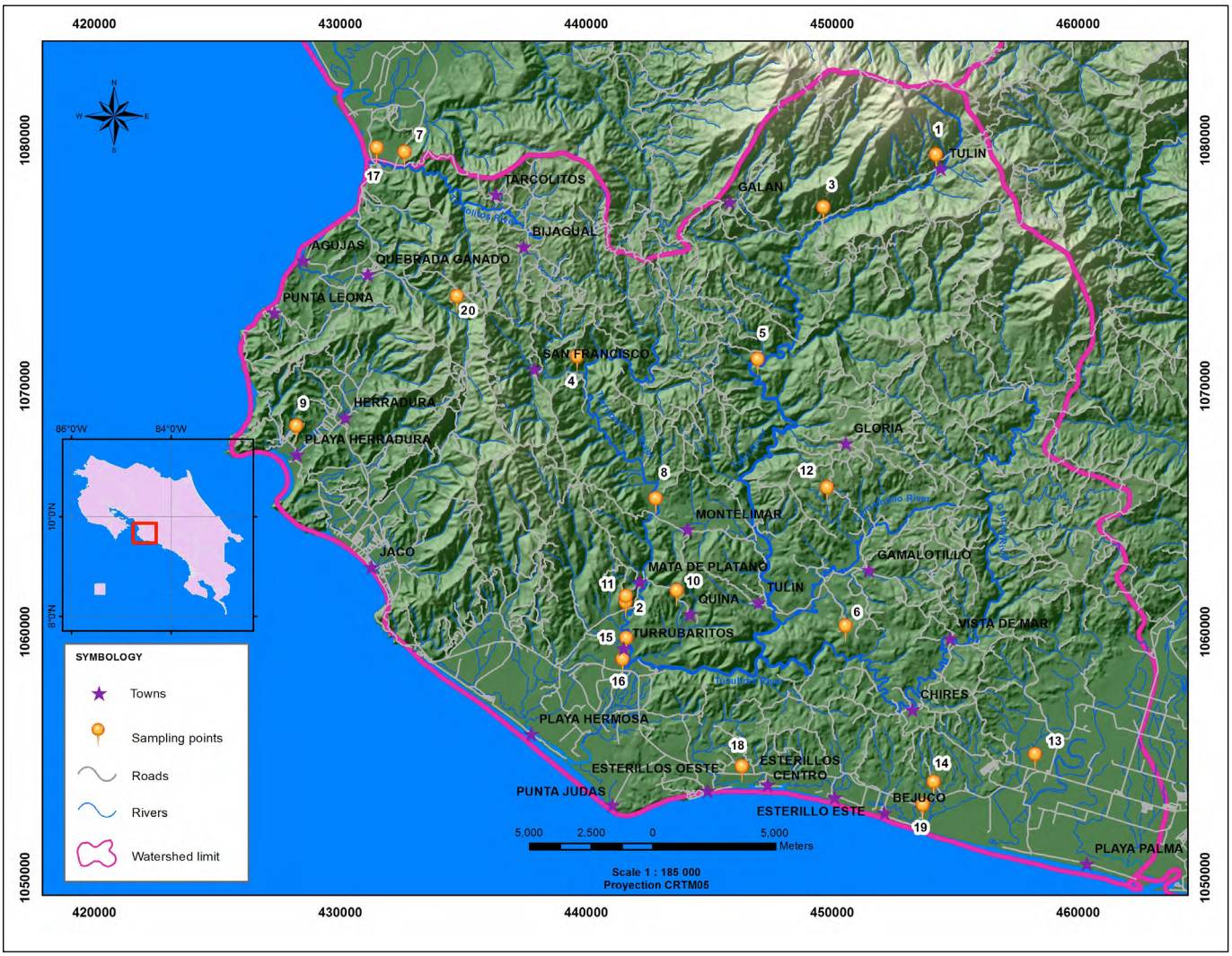

Figure 1. Map showing the sampled localities in the Tusubres River basin, Pacific coast, Costa Rica; associate data is provided in Table 1.

frame and 1 mm net mesh size and 35×50 cm frame and 5 mm net mesh size), cast nets (1.2 m and 2.3 m radius and 15 mm net mesh size), gill nets (20×1.8 m and 2 and 5 cm between knots), seine nets (6×2 m and 10×2 m and 5 mm between knots), and a Smith-Root LR-20B® backpack electrofisher. Eleven sampling events were conducted: February and November 2011, February and November 2012, February, March, May, August and November 2013, and February and October 2014. Fishing gear was selected according to the environmental and hydrological conditions at each site. Collection and research permits (No-181-2010-SINAC, No 157-2012-SINAC and No 007-2013-SINAC) were issued by the Costa Rican Ministerio de Ambiente y Energía (MINAE) and the Sistema Nacional de Áreas de Conservación (SINAC).

The majority of the captured specimens were identified in the field following Bussing (1998) and Robertson and Allen (2008); these specimens were released alive. Some specimens of uncertain field identification were retained and were first preserved in 10% formalin and then transferred to 70% ethanol for laboratory identification. Prior to preservation, specimens captured alive were anaesthetized and euthanized with clove oil following Inoue et al. (2003). Voucher specimens (at least one) of all sampled species were retained, photographed (Figures 2–5) and deposited at the fish collection of the Museo de Zoología of the Universidad de Costa Rica (UCR) with catalog numbers provided in Table 3. In order to supplement the data obtained through this inventory, a thorough review of the material deposited at the fish collection of the UCR was also conducted (Table 2).

Ichthyofaunal data were recorded as presence-absence of individual fish species by sampled sites (Table 3). The family tolerance to salinity is listed (Table 3) according to the classification of Myers (1949). Taxonomic nomenclature follows Eschmeyer (2015). Measurements and counts follow Hubbs and Lagler (1958) and Bussing (1998).

RESULTS

A total of 50 species, and 2384 specimens, were collected; representing 43 genera and 24 families (Table 3). The families with highest species richness were Eleotridae (6 spp., 11.1%), Gobiidae (6 spp., 11.1%), Poeciliidae (5 spp., 9.3%) and Characidae (4 spp., 7.4%).

Four species (*Achirus mazatlanus* (Steindachner 1869), Achiridae; *Hypsoblennius maculipinna* (Regan 1903), Blenniidae; *Halichoeres aestuaricola* Bussing 1972, Labridae; and *Microdesmus dorsipunctatus* Dawson 1968, Microdesmidae), all with voucher specimens deposited at the UCR collection, were added to the list of species for the river basin (Table 3). From the review of the UCR material, a total of 35 species were recorded; representing 32 genera and 18 families (Table 3), including these four species.

Taking into consideration both sources of information (fish inventory and UCR material), the fish fauna of the Tusubres River Basin is comprised of a total of 54 species; representing 47 genera and 27 families (Table 3). Based on Bussing (1998), all listed species were native to the Tusubres River Basin. The number of species at a single locality ranged from 2 to 23 (mean=11.8). Highest species richness (12–23 species, mean=17.8) was recorded very close to the coast, between 9 and 14 m above sea level. Upstream, between 106 and 455 m, the number of species was relatively lower (8–17, mean=10.8), with localities 6, 11 and 12 (see Figure 1) having the low richness values (2–3 species, mean=2.33)

Based on Myers's (1949) salinity tolerance classification of freshwater fishes, the majority of species were peripheral (35 species, 64.8%), followed by secondary freshwater fishes (11 species, 20.4%). Only four families (Characidae, Gymnotidae, Heptapteridae and Lebiasinidae) and 8 species (about 14.8% of the total fish diversity) of primary freshwater fishes were recorded (Table 3).

On the basis of Bussing (1987, 1998) and Angulo et al. (2013), a total of two species (*Caranx sexfasciatus* Quoy & Gaimard 1825, Carangidae; and *Opisthonema libertate* (Günther 1867), Clupeidae) were considered to be new records for Costa Rican inland waters. In addition, on the basis of Bussing (1987, 1998), two species (*Gymnotus maculosus* Albert & Miller 1995, Gymnotidae; and *Lebiasina boruca* (Bussing 1967), Lebiasinidae) were shown to have expanded ranges.

Key to species of fishes from the Tusubres River basin, Pacific coast, Costa Rica

The following key is based on our research and data available in the literature (Bussing 1987, 1998; Nelson 2006; Robertson and Allen 2008).

Table 2. Sampled localities in the Tusubres River basin, Pacific coast, Costa Rica, with voucher specimens at the UCR collection (examined lots), prior to this inventory.

UCR	Locality	Latitude (N)	Longitude (W)	Altitude (m)	Date	Collectors	Lots examined
0305/06	Quebrada Visita, 4 km E of Esterillos	09°31'30.00"	084°25'04.00"	14	16-Jan-69	W.A. Bussing, R. Nishimoto, J. Perry, C. Mata	16
0308	Estero Aserradero, 3.5 km W of Esterillos	09°31'50.00"	084°29'19.68"	10	17-Jan-69	W.A. Bussing, R. Nishimoto, J. Perry, C. Mata	20
1368	Río Tusubres, 300 m upstream from Jacó-Esterillos road	09°34'40.00"	084°31'54.01"	14	26-Mar-82	W.A. Bussing	12
1471	Quebrada Cañablancal, 1 km E of the Herradura Beach	09°39'20.00"	084°39'14.76"	33	15-Apr-83	W.A. Bussing	7

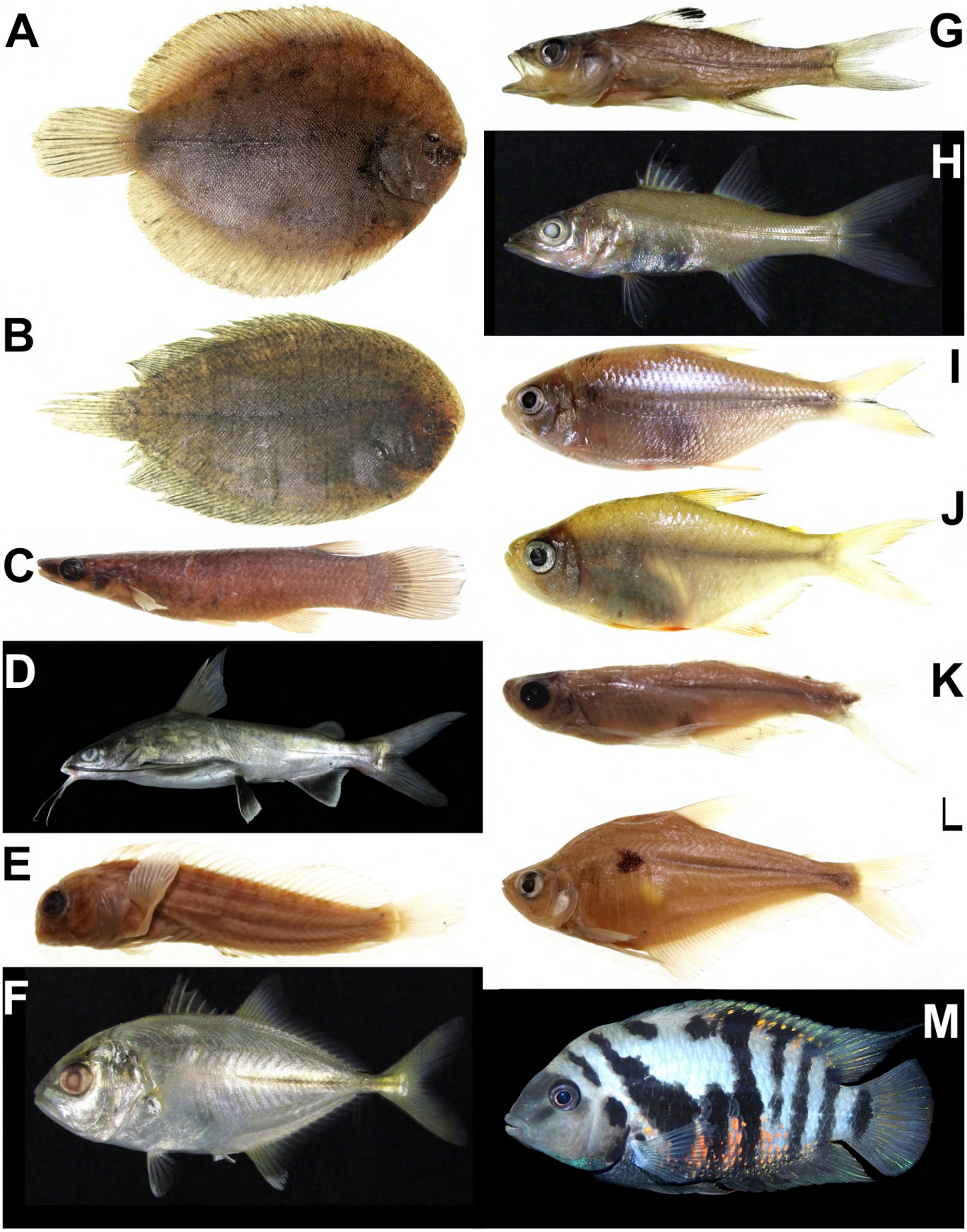

Figure 2. Fishes from the Tusubres River basin, Pacific coast, Costa Rica. **A**) *Achirus mazatlanus*; **B**) *Trinectes fonsecensis*; **C**) *Oxyzygonectes dovii**; **D**) *Sciades seemanni*; **E**) *Hypsoblennius maculipinna**; **F**) *Caranx sexfasciatus*; **G**) *Centropomus nigrescens**; **H**) *C. unionensis*; **I**) *Astyanax aeneus*; **J**) *Hyphessobrycon savagei*; **K**) *Pterobrycon myrnae**; **L**) *Roeboides ilseae**; **M**) *Amatitlania siquia*. *Pictures taken after fixation in 10% formalin and stored in 70% alcohol. Voucher specimens are listed in Table 3.

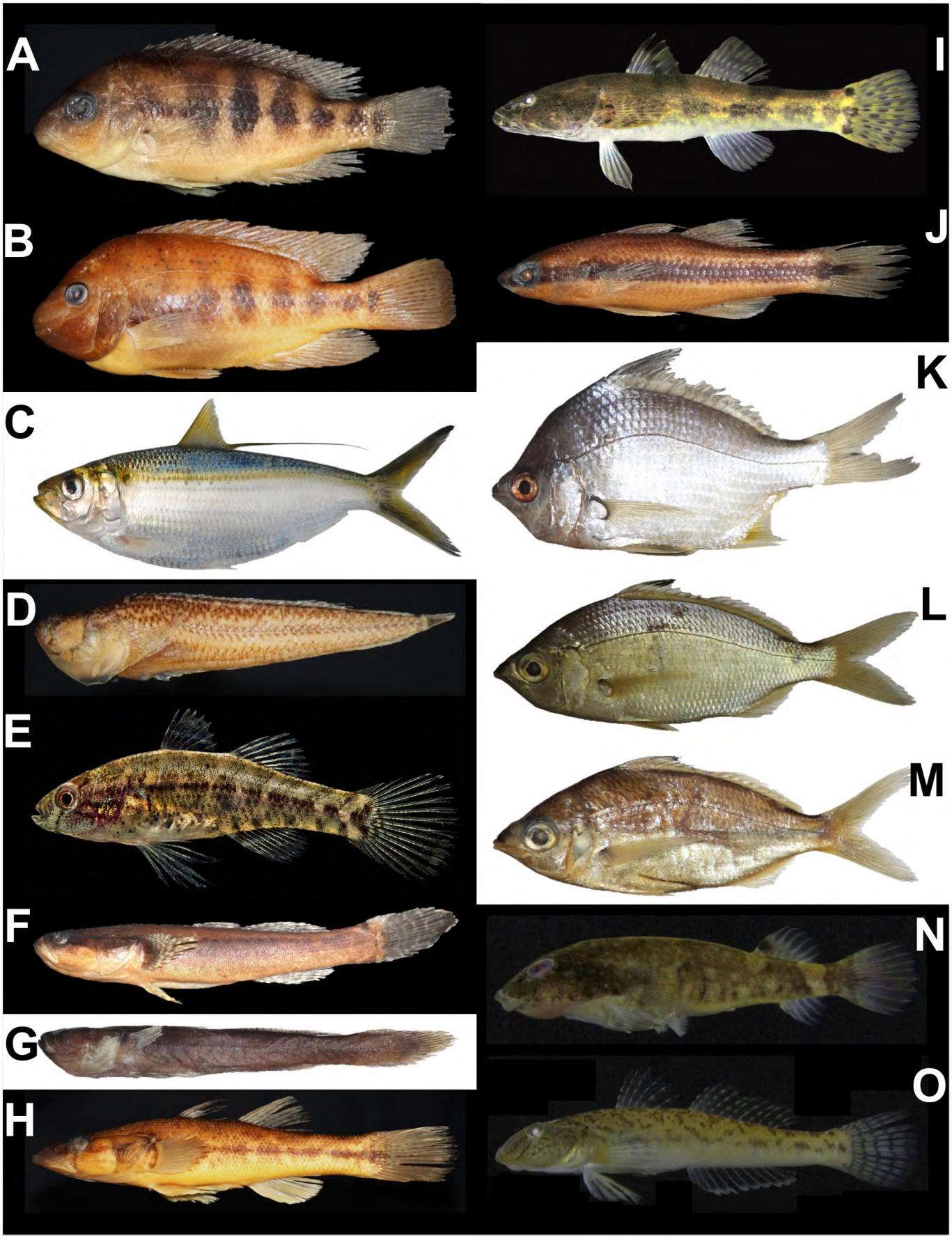

Figure 3. Fishes from the Tusubres River basin, Pacific coast, Costa Rica, continuation. **A**) *Amphilophus diquis**; **B**) *Tomocichla sieboldii**; **C**) *Opisthonema libertate*; **D**) *Dactyloscopus amnis**; **E**) *Dormitator latifrons*; **F**) *Eleotris picta**; **G**) *Erotelis armiger**; **H**) *Gobiomorus maculatus**; **I**) *G. polylepis*; **J**) *Hemieleotris latifasciata**; **K**) *Diapterus peruvianus*; **L**) *Eucinostomus currani**; **M**) *Gerres simillimus**; **N**) *Gobiesox potamius*; **O**) *Awaous transandeanus*. *Pictures taken after fixation in 10% formalin and stored in 70% alcohol. Voucher specimens are listed in Table 3.

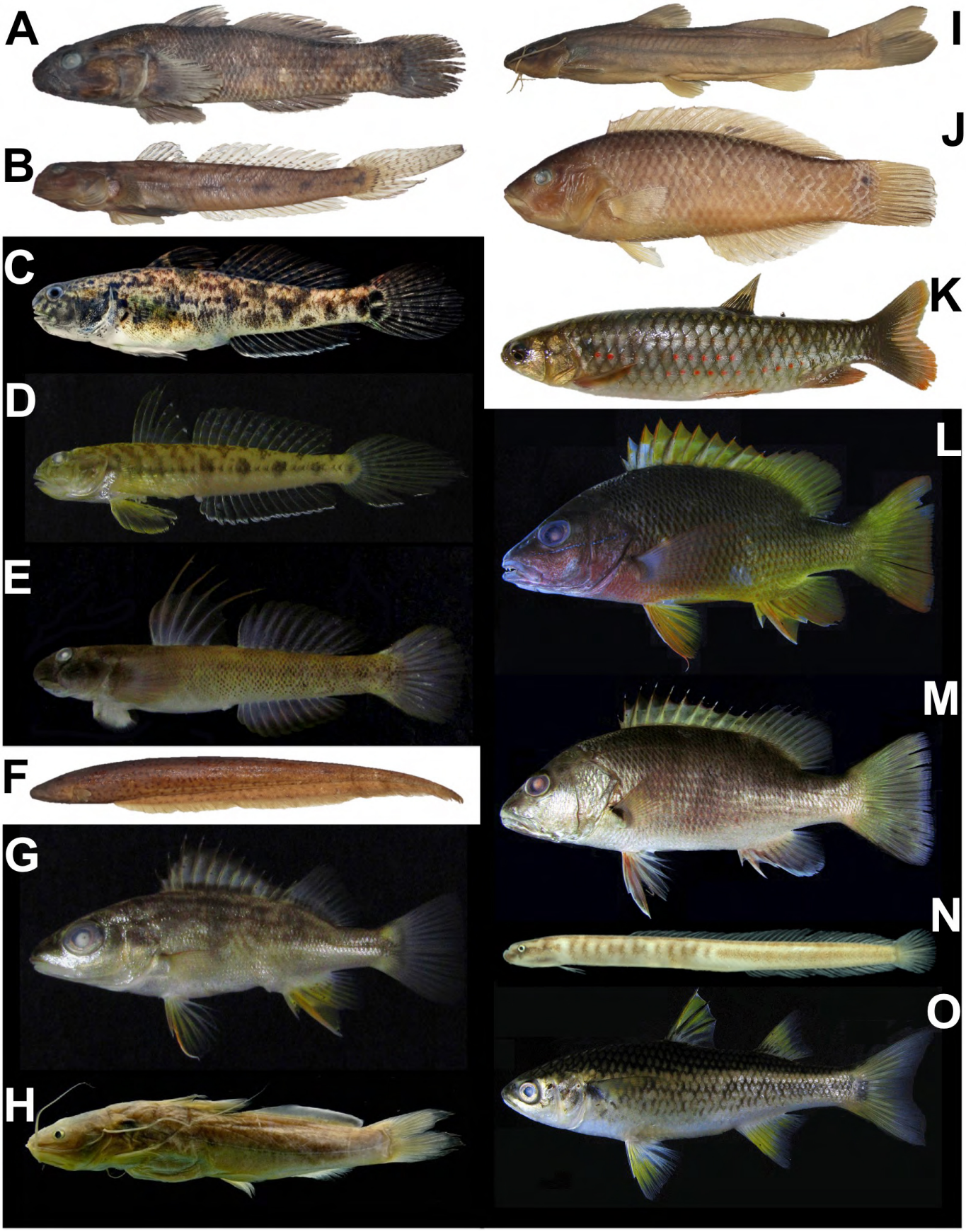

Figure 4. Fishes from the Tusubres River basin, Pacific coast, Costa Rica, continuation. **A**) *Bathygobius andrei**; **B**) *Ctenogobius sagittula**; **C**) *Evorthodus minutus*; **D**) *Gobionellus microdon*; **E**) *Sicydium salvini*; **F**) *Gymnotus maculosus**; **G**) *Pomadasys bayanus*; **H**) *Rhamdia guatemalensis**; **I**) *R. laticauda**; **J**) *Halichoeres aestuaricola**; **K**) *Lebiasina boruca*; **L**) *Lutjanus argentiventris*; **M**) *L. novemfasciatus*; **N**) *Microdesmus dorsipunctatus**; **O**) *Agonostomus monticola*. *Pictures taken after fixation in 10% formalin and stored in 70% alcohol. Voucher specimens are listed in Table 3.

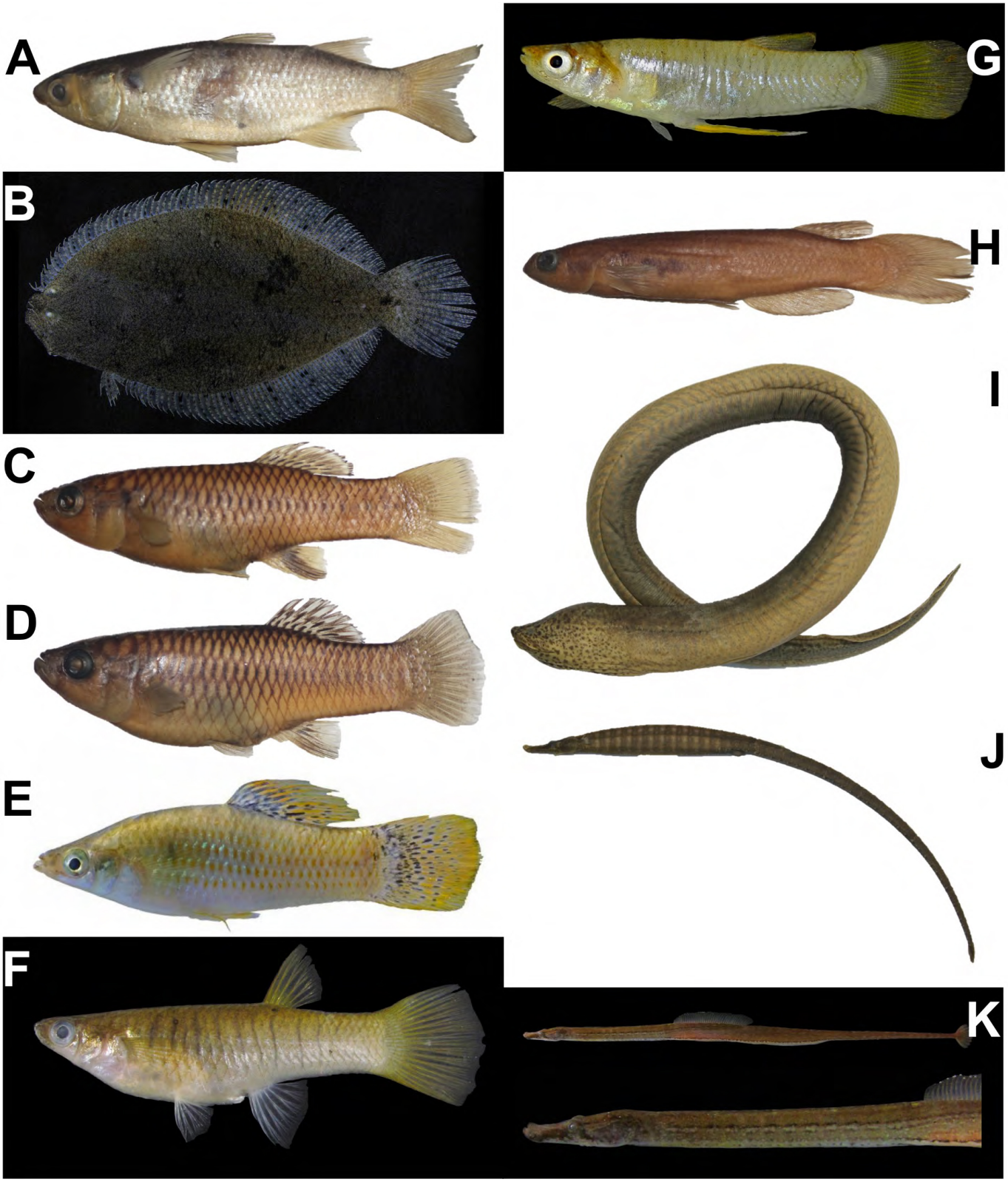

Figure 5. Fishes from the Tusubres River basin, Pacific coast, Costa Rica, continuation. **A**) *Mugil curema**; **B**) *Citharichthys gilberti*; **C**) *Brachyrhaphis olomina**; **D**) B. *rhabdophora**; **E**) *Poecilia gillii*; **F**) *Poeciliopsis elongata*; **G**) *P. turrubarensis*; **H**) *Cynodonichthys isthmensis**; **I**) *Synbranchus marmoratus**; **J**) *Pseudophallus elcapitanensis**; **K**) *Pseudophallus starksii*. *Pictures taken after fixation in 10% formalin and stored in 70% alcohol. Voucher specimens are listed in Table 3.

Table 3. Fish fauna, by sampled localities, in the Tusubres River basin, Pacific coast, Costa Rica. After family names (in bold) the number of genera and species, separated by a comma, are indicated. UCR=Specimens with voucher at UCR, prior fieldwork. Tol.=Tolerance to salinity based on Meyers (1949); primary=Pri; secondary=Sec; and peripheral=Per. Fig.=Reference to Figure. Voucher specimens deposited at UCR; by each species catalog number is indicated.

	Localities																					
Family/Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**UCR**	**Tol.**	**Fig.**	**Voucher**
Achiridae 2, 2																					**Per**		
Achirus mazatlanus (Steindachner, 1869)																			X	X		2A	3080002
Trinectes fonsecensis (Günther, 1862)		X																	X			2B	3080003
Anablepidae 1, 1																					**Sec**		
Oxyzygonectes dovii (Günther, 1866)																X		X	X	X		2C	0308012
Ariidae 1, 1																					**Per**		
Sciades seemanni (Günther, 1864)																	X					2D	2949001
Bleniidae 1, 1																					**Per**		
Hypsoblennius maculipinna (Regan, 1903)																				X		2E	0308016
Carangidae 1,1																					**Per**		
Caranx sexfasciatus Quoy & Gaimard, 1825																	X	X	X			2F	2958005
Centropomidae 1, 2																					**Per**		
Centropomus nigrescens Günther, 1864		X			X											X		X	X	X		2G	0308018
Centropomus unionensis Bocourt, 1868																	X		X			2H	2958002
Characidae 4, 4																					**Pri**		
Astyanax aeneus (Günther, 1860)	X	X	X	X	X		X	X	X	X			X	X	X					X		2I	3082001
Hyphessobrycon savagei Bussing, 1967					X					X				X						X		2J	3082002
Pterobrycon myrnae Bussing, 1974						X								X						X		2K	3082005
Roeboides ilseae Bussing, 1986					X		X	X	X				X	X						X		2L	0306009
Cichlidae 3, 3																					**Sec**		
Amatitlania siquia Schmitter-Soto, 2007					X				X	X			X	X								2M	3082003
Amphilophus diquis (Bussing, 1974)					X									X						X		3A	0305002
Tomocichla sieboldii (Kner, 1863)	X	X	X	X	X		X															3B	3082004
Clupeidae 1, 1																					**Per**		
Opisthonema libertate (Günther, 1867)																			X			3C	3080004
Dactyloscopidae 1, 1																					**Per**		
Dactyloscopus amnis Miller, & Briggs 1962																		X		X		3D	0308007
Eleotridae 5, 6																					**Per**		
Dormitator latifrons (Richardson, 1844)														X	X	X	X	X		X		3E	2962001
Eleotris picta Kner, 1863		X			X		X			X				X	X	X	X	X	X	X		3F	2963002
Erotelis armiger (Jordan & Richardson, 1895)																			X	X		3G	0308004
Gobiomorus maculatus (Günther, 1859)		X			X		X		X	X			X	X	X	X	X	X	X	X		3H	2956002
Gobiomorus polylepis Ginsburg, 1953									X						X	X	X			X		3I	2956001
Hemieleotris latifasciata (Meek & Hildebrand, 1912)														X	X	X	X	X		X		3J	2963001
Gerreidae 3, 3																					**Per**		
Diapterus peruvianus (Cuvier, 1830)																X		X				3K	3080001
Eucinostomus currani Zahuranec, 1980		X														X	X	X	X	X		3L	2946001
Gerres simillimus Regan, 1907																X		X	X	X		3M	0308021
Gobiesocidae 1, 1																					**Per**		
Gobiesox potamius Briggs, 1955				X				X									X					3N	2955003
Gobiidae 6, 6																					**Per**		
Awaous transandeanus (Günther, 1861)	X	X	X	X	X		X	X	X					X			X			X		3O	2946002

Continued

Table 3. *Continued.*

	Localities																					
Family/Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**UCR**	**Tol.**	**Fig.**	**Voucher**
Bathygobius andrei (Sauvage, 1880)																X	X	X	X	X		4A	2958001
Ctenogobius sagittula (Günther, 1862)																X		X	X	X		4B	0308002
Evorthodus minutus Meek & Hildebrand, 1928																			X	X		4C	0308001
Gobionellus microdon (Gilbert, 1892)																	X					4D	2962002
Sicydium salvini Ogilvie-Grant, 1884		X	X		X		X										X					4E	2955002
Gymnotidae 1, 1																					**Pri**		
Gymnotus maculosus Albert & Miller, 1995						X																4F	3081001
Haemulidae 1, 1																					**Per**		
Pomadasys bayanus Jordan & Evermann, 1898		X															X	X				4G	2954001
Heptapteridae 1, 2																					**Pri**		
Rhamdia guatemalensis (Günther, 1864)		X	X	X	X		X	X		X			X	X								4H	3083003
Rhamdia laticauda (Kner, 1858)	X			X	X		X		X	X			X									4I	3083002
Labridae 1, 1																					**Per**		
Halichoeres aestuaricola Bussing, 1972																				X		4J	0308017
Lebiasinidae 1, 1																					**Pri**		
Lebiasina boruca (Bussing, 1967)										X												4K	3083001
Lutjanidae 1, 2																					**Per**		
Lutjanus argentiventris (Peters, 1869)		X														X	X	X	X	X		4L	0308013
Lutjanus novemfasciatus Gill, 1862		X														X	X	X	X	X		4M	2958004
Microdesmidae 1, 1																					**Per**		
Microdesmus dorsipunctatus Dawson, 1968																				X		4N	0308006
Mugilidae 2, 2																					**Per**		
Agonostomus monticola (Bancroft, 1834)	X	X	X	X	X		X	X	X						X	X	X			X		4O	2956003
Mugil curema Valenciennes, 1836															X	X		X	X	X		5A	0308019
Paralichthyidae 1, 1																					**Per**		
Citharichthys gilberti Jenkins & Evermann, 1889																	X		X	X		5B	2948001
Poeciliidae 3, 5																					**Sec**		
Brachyrhaphis olomina (Meek, 1914)							X															5C	3084001
Brachyrhaphis rhabdophora (Regan, 1908)	X		X	X	X					X	X	X	X	X						X		5D	0308009
Poecilia gillii (Kner, 1863)	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X			X		5E	0305001
Poeciliopsis elongata (Günther, 1866)																	X	X				5F	2958003
Poeciliopsis turrubarensis (Meek, 1912)		X									X				X	X	X		X	X		5G	0308008
Rivulidae 1, 1																					**Sec**		
Cynodonichthys isthmensis (Garman, 1895)	X			X								X										5H	3085001
Synbranchidae 1, 1																					**Sec**		
Synbranchus marmoratus Bloch, 1795		X						X	X					X						X		5I	0305005
Syngnathidae 1, 2																					**Per**		
Pseudophallus elcapitanensis (Meek & Hildebrand, 1914)					X				X						X			X		X		5J	1368012
Pseudophallus starksii (Jordan & Culver, 1895)									X				X		X		X			X		5K	2955004
TOTAL (Species)	8	17	8	10	17	2	12	8	12	10	3	2	9	15	12	18	23	19	20	35		54	54

1 Body asymmetrical, both eyes on the same side of head 2
1′ Body symmetrical, one eye on each side of head . 4

2 Pigment and eyes on the left side of fish (Paralichthyidae); teeth equally developed on both sides of jaws, in 1 series of immovable teeth on each jaw, no canines but front teeth slightly enlarged; gill rakers slender, moderately long, lower rakers 12–15; eye side pectoral fin 43–59% of head length ..... *Citharichthys gilberti* (Figure 5B)
2′ Pigment and eyes on right side of fish (Achiridae) 3

3 Interbranchial foramen present; dorsal fin rays 55–57; scales on eyed side with black hair-like filaments ..... *Achirus mazatlanus* (Figure 2A)
3′ Interbranchial foramen absent; dorsal fin rays 58–60; scales on eyed side without black hair-like filaments ..... *Trinectes fonsecensis* (Figure 2B)

4 Dorsal, caudal and pelvic fins absent 5
4′ Dorsal, caudal and pelvic fins present 8

5 Body covered by bony plates (Syngnathidae) 6
5′ Body without bony plates, naked or with normal scales 7

6 Dorsal fin rays 37–44; snout short 35–37% of head length; head with a dark lateral stripe ..... *Pseudophallus elcapitanensis* (Figure 5J)
6′ Dorsal fin rays 30–35; snout long 38–43% of head length; head without marks ..... *Pseudophallus starksii* (Figure 5K)

7 Pectoral and anal fins present; scales present (Gymnotidae); scales above the lateral line large, 6–8 rows above the lateral line at a distance equidistant between the head and the tip of the tail; flanks and belly generally with brown blotches two to four times the diameter of the eye ..... *Gymnotus maculosus* (Figure 4F)
7′ Pectoral and anal fins absent; scales absent (Synbranchidae); general coloration grayish brown or yellowish brown, being darker above and paler with dark speckles of variable size ventrally ..... *Synbranchus marmoratus* (Figure 5I)

8 Pelvic fins united into an adhesive disc 9
8′ Pelvic fins separated, not in form of an adhesive disc 15

9 Upper part of adhesive disc formed by part of pectoral fins; body naked (Gobiesocidae); tadpole shaped, head broad, depressed, with sensory papillae; upper lip broad, much wider at front than at sides; upper jaw with a deep patch of conical teeth at front; eye diameter 41–47% of interorbital distance ..... *Gobiesox potamius* (Figure 3N)
9′ Pectoral fins normal, not forming part of adhesive disc; body scaled (Gobiidae) 10

10 Uppermost 6 pectoral fin rays forming free filaments, first to fourth branch only once; scales large, rough, present on midline of nape; body grey brown with light streak on each scale; faint dark bars and blotches evident on side; head without pale spots; first dorsal fin with an oblique dark bar at front; 3 dark blotches behind eye small, the second is smallest and third is largest ..... *Bathygobius andrei* (Figure 4A)
10′ Uppermost pectoral fin rays not forming free filaments; scales variable in size, rough to smooth, absent on midline of nape 11

11 5 or 6 pores above the preopercle and opercle, behind the eye; shoulder girdle with elongated dermal papillae under the opercle; scales in lateral series 56–61; transverse scales, between origin of second dorsal fin and anal fin base, 16–19 ..... *Awaous transandeanus* (Figure 3O)
11′ 3 or 4 pores above the preopercle and opercle, behind the eye; shoulder girdle without elongate dermal papillae under the opercle 12

12 Mouth inferior, located below the snout; pelvic fins usually fused with belly; pelvic fin rays with numerous thick branches; general coloration gray or greenish brown above, yellowish below ..... *Sicydium salvini* (Figure 4E)
12′ Mouth terminal, located at the end of snout; pelvic fins not fused with belly; pelvic fin rays with few thick branches 13

13 A single pore behind eye and another over the edge of preopercle; teeth with flattened, forked tips; scales large, rough at rear of body, smooth at front, present on sides of head, 28–30 in lateral series; body grey-brown, head darker, rear body red brown; sides with irregular dark blotches forming bars; tail base with 2 dark spots; spiny dorsal with round dark spot at base and longest spines with black tips; soft dorsal red, with black stripes; anal fin red ..... *Evorthodus minutus* (Figure 4C)
13′ A single pore behind eye and another 2 or 3 over the edge of preopercle; teeth conical 14

14 Head pores extending above the preopercle; an oblique row of papillae posteriorly on opercle; body color light tan with 4 dark brown blotches along middle of side and a dark brown spot at middle of caudal fin base; a brown stripe on cheek and a brown blotch just behind on center of gill cover; second dorsal and caudal fin with brown spots ..... *Ctenogobius sagittula* (Figure 4B)

14′ Head pores extending above the opercle; an vertical row of papillae posteriorly on opercle; body color light tan with a silvery sheen on opercle, chest and belly; irregular brown saddles on back; flank with a row of dark blotches separated by dark spots; dorsal and caudal fins with rows of spots forming stripes and bars, respectively ..... *Gobionellus microdon* (Figure 4D)

15 Fins without spines 16
15′ One or more fins with spines 28

16 Adipose fin present 17
16′ Adipose fin absent 21

17 Anal fin rays 8 or 9 (Lebiasinidae); body elongate, compressed and fusiform; dorsal profile nearly straight or arching slightly; jaws with teeth; lower jaw protruding beyond upper; scales in lateral series 26 or 27; coloration gray above and on flanks and whitish below, with 3 longitudinal red stripes on each side formed by a red blotch on each scale of the 3 lateral rows ..... *Lebiasina boruca* (Figure 4K)
17′ Anal fin rays 20–50 (Characidae) 18

18 Nape concave; two pairs of external teeth on premaxillary; anal fin very long, with 41–50 rays; humeral spot well developed and covering 4 or more longitudinal scales and 6 or more vertical scales in adults ..... *Roeboides ilseae* (Figure 2L)
18′ Nape convex or straight; no external teeth on premaxillary; anal fin short, with 20–30 rays 19

19 Dorsal fin origin behind origin of anal fin; greatest body depth less than 32% of standard length; mature males with two pairs of enlarged humeral scales ..... *Pterobrycon myrnae* (Figure 2K)
19′ Dorsal fin origin anterior to origin of anal fin; greatest body depth usually more than 32% of standard length; scales normal 20

20 A singe vertical humeral spot; a black blotch, usually rhomboidal, on base of tail ..... *Astyanax aeneus* (Figure 2I)
20′ 2 vertical humeral spots of equal intensity, separated by a paler interspace; no conspicuous dark blotch on base of tail ..... *Hyphessobrycon savagei* (Figure 2J)

21 Abdomen compressed and with a row of scutes along the ventral midline; caudal fin forked (Clupeidae); dorsal at about midpoint of body, last ray long and filamentous; anal fin with base shorter than head; lower gill rakers 63–110; rear of gill opening on body with 2 fleshy lobes; pectoral long, passing origin of dorsal fin ..... *Opisthonema libertate* (Figure 3C)
21′ Abdomen not compressed and without ventral scutes; caudal fin rounded 22

22 Eyes with free borders; males with anal fin modified into a gonopodium; third ray of anal fin not branched (Poeciliidae) 23
22′ Eyes with or without free borders; males with normal anal fin; third ray of anal fin (counting rudiments) branched 27

23 Anal fin with a black blotch 24
23′ Anal fin clear or dusky, without a black blotch 25

24 A series of 9–11 small squares along the median lateral length of the body forming broadened part of the vertical bars (very diffuse squares in large females); 9–12 subterminal spines in ray 4p of the gonopodium (sensu Bussing 1998) of large mature males (see) ..... *Brachyrhaphis olomina* (Figure 5C)
24′ The series of small lateral squares very diffuse or absent; 6–8 subterminal spines in ray 4p of the gonopodium (sensu Bussing 1998) of large mature males (see Bussing 1998) ..... *Brachyrhaphis rhabdophora* (Figure 5D)

25 Pelvic fins of mature males modified, tip of first ray with a soft swelling, second ray thickened; gonopodium short, rarely reaching to mid-dorsal fin; dorsal fin origin of females usually above anal fin origin; dorsal fin usually with black spotting or a blotch proximally; cross-hatch pattern faint; caudal fin profusely spotted on base, often on entire fin; rows of yellow or black spots along sides ..... *Poecilia gillii* (Figure 5E)
25′ Pelvic fins not modified in males; gonopodium long, extending nearly to a point below tip of dorsal fin; dorsal fin origin of females arising behind anal fin origin; dorsal fin usually without black spotting or a blotch proximally; cross-hatch pattern on body prominent 26

26 Total gill rakers 29–32; pectoral fin long, usually reaching middle of pelvic fin and to within an eye diameter of dorsal-fin origin ..... *Poeciliopsis elongata* (Figure 5F)
26′ Total gill rakers 15–22; pectoral fin short, usually not extending to middle of pelvic fin, nor within an eye diameter of dorsal-fin origin ..... *Poeciliopsis turrubarensis* (Figure 5G)

27 Eyes with free borders (Anablepidae), the upper part silvery; predorsal profile straight; body color gray, becoming pearl and white on the abdomen; fins usually yellow; mature males with dark brown bars on the posterior half of the flanks ..... *Oxyzygonectes dovii* (Figure 2C)
27′ Eyes without free borders (Rivulidae), the upper part usually brown, never silvery; predorsal profile curved; predorsal scales 25–33; body color brown with fins of the same color; mature males with a

dark humeral blotch, horizontally elongate and surrounded by golden or copper colored scales, females usually only with an caudal ocellus ..... *Cynodonichthys isthmensis* (Figure 5H)

28 Two or more pairs of barbels around mouth; body naked 29
28′ No barbels around mouth; body covered with scales 31

29 Length of adipose fin base less than half of head length (ARIIDAE); anal fin rays 17–20; head shield granular, the rough portion extending forward as broad triangular patch on each side of flattened, smooth area between eyes; central head groove well-defined, narrow, deep, but relatively short and not extending to base of bony nape process; bony nape process triangular with bluntly rounded apex; eye large, 36–63% of interorbital distance .. *Sciades seemanni* (Figure 2D)
29′ Length of adipose fin base greater than head length (Heptapteridae); anal fin rays 11–15 29

30 Maxillary barbels long, usually extending beyond origin of dorsal fin; serrations present on both margins of pectoral spines ..... *Rhamdia guatemalensis* (Figure 4H)
30′ Maxillary barbels short, not extending beyond pectoral fins; serrations present only on inner (posterior) margin of pectoral spines, sometimes without serrations ... *Rhamdia laticauda* (Figure 4I)

31 Pelvic fins subabdominal, inserted well behind pectoral fin bases, with one spine and 5 branched soft rays; 2 dorsal fins (Mugilidae) 32
31′ Pelvic fins thoracic, inserted in advance of or below pectoral fins base; 2 or a single dorsal fin 33

32 Eyes not covered by a transparent adipose eyelid; second dorsal fin with 9 rays; anal fin with 2 spines and 10 rays; body color olive above, white below, with a dark crisscrossed lines on back; fins yellowish; upper third of pectoral fin base dark; a dark blotch on tail base; juveniles with a distinct spot on tail ..... *Agonostomus monticola* (Figure 4O)
32′ Eyes mostly covered by a well developed transparent adipose eyelid; second dorsal fin with a single spine and 8 rays; anal fin with 3 spines and 9 rays (10 in juveniles); body color olive to bluish, silvery on sides, white below; a small black blotch at upper base of pectoral fin; anal and pelvic fins yellowish, tail may be yellowish at base, with dark border ..... *Mugil curema* (Figure 5A)

33 Two dorsal fins 34
33′ A single dorsal fin 43

34 Lateral line absent; caudal fin rounded (Eleotridae) 35
34′ Lateral line present; caudal fin forked 40

35 Scales in lateral series 90–110; body color dark brown, paler below, covered with fine black dots ... *Erotelis armiger* (Figure 3G)
35′ Scales in lateral series 25–82 36

36 Head compressed; eyes on side of head; scales in lateral series 25–36 37
36′ Head depressed; eyes on top of head; scales in lateral series 56–82 38

37 Head scaled; gill rakers well developed; first dorsal fin with 7 weak spines; body color brown to purplish, with a prominent blue spot behind upper edge of gill cover ... *Dormitator latifrons* (Figure 3E)
37′ Head without scales; gill rakers small and poorly developed; first dorsal fin with 6 weak spines; body color greenish brown, with sides yellowish and belly whitish, and with a dark band bordered above and below by iridescent greenish yellow stripes extending from tip of snout to the middle of tail ... *Hemieleotris latifasciata* (Figure 3J)

38 Vomer without teeth; gill openings extending forward to below preopercular margin, well behind the eyes; an embedded spine at posteroventral angle of preopercle; scales in lateral series 60-68; transverse scales, between second dorsal fin origin and base of anal fin, 21–24 *Eleotris picta* (Figure 3F)
38′ Vomer with teeth; gill openings extending forward to below eyes; no spine at angle of preopercle; scales in lateral series 56–61 or 74–82 39

39 Pectoral fin rays 15–16; scales in lateral series 56–61 ..... *Gobiomorus maculatus* (Figure 3H)
39′ Pectoral fin rays 18–19; scales in lateral series 74–82 ..... *Gobiomorus polylepis* (Figure 3I)

40 Lateral line not extending to the end of caudal fin, scales at rear of lateral line forming spiny, plate-like scutes; caudal fin base slender (Carangidae); second dorsal fin large, with 19–22 rays; anal fin large, with 15–17 rays; dorsal and anal fin with long anterior lobes ..... *Caranx sexfasciatus* (Figure 2F)
40′ Lateral line extending to end of caudal fin, scales at rear part of lateral line not forming spiny, plate-like scutes; caudal fin base thick (Centropomidae); second dorsal fin short, with 9–11 rays; anal fin short, with 6 rays; dorsal and anal fin without long anterior lobes 41

41 Lateral line black; second dorsal fin rays 9 (rarely 10); second and third anal spines relatively short, about equal in length, not exceeding longest anal ray ..... *Centropomus nigrescens* (Figure 2G)
41′ Lateral line clear; second dorsal fin rays 10 (rarely

9 or 11); second anal spine much stouter than third spine and slightly longer, also exceeding longest anal soft ray, almost reaching to tail fin ..... *Centropomus unionensis* (Figure 2H)

42 Head large, flattened above, rounded and narrow anteriorly; eyes dorsal, protrusible, on short stalks, without papillae; mouth extremely oblique; both lips with skin flaps; lower jaw protruding (Dactyloscopidae); dorsal fin with 11–14 spines and 23–27 rays; anal fin with 2 spines and 28-32 rays; dorsal and anal fins joined by membranes to caudal fin base ..... *Dactyloscopus amnis* (Figure 3D)

42′ Head variable in length and shape, not as above; eyes on side of head, not protrusible; mouth variable, not extremely oblique; lips without skin flaps 43

43 Body naked; a short, pointed cirrus on rear nostril and a short (less than eye diameter), branched cirrus over eye (Blenniidae); gill openings restricted to sides of body by fusion of gill membranes to throat; dorsal fin with 12 spines, 14 rays, and a slight notch between the spiny and soft parts; anal fin rays with 2 spines and 16 rays; last rays of dorsal and anal fins joined by membranes to base of tail fin; dorsal fin with a dark stripe covering its outer half along the first 3-4 spines ..... *Hypsoblennius maculipinna* (Figure 2E)

43′ Body scaled; no cirri on head 44

44 Body slender, wormlike (Microdesmidae), its height less than 10% of standard length; snout rounded; lower jaw strongly projecting, with a small fleshy lump at chin; gill opening large (not tubular), longer than base of pectoral fin; dorsal fin with 15-17 spines evenly spaced and 38-43 rays; anal fin with 2 spines and 34–38 rays; pectoral fin rays 12–14 ..... *Microdesmus dorsipunctatus* (Figure 4N)

44′ Body not wormlike, its height more than 10% of standard length; snout pointed to rounded; lower jaw not strongly projecting, without a small fleshy lump at chin 45

45 Nasal openings simple, one on each side of head; lateral line discontinuous (Cichlidae) 46

45′ Nasal openings double on each side of head; lateral line continuous 48

46 Predorsal profile convex; mouth subinferior; teeth of outer row spatulate and bicuspid, with a small denticle or spur on the lingual side; anal fin spines 4–5 ..... *Tomocichla sieboldii* (Figure 3B)

46′ Predorsal profile nearly straight to convex; mouth terminal or subterminal; teeth of outer row sharp, conical and cylindrical, unicuspid; anal fin spines 5–10 47

47 Dorsal fin with 17–18 spines and 8–10 rays; anal fin with 9–10 spines and 7–8 rays; first bar on side of body, "Y" shaped, well marked, caudal arm discontinuous; opercle with a black blotch on the upper half; no small pale blue spots on soft dorsal rays and caudal fin ..... *Amatitlania siquia* (Figure 2M)

47′ Dorsal fin with 15–17 spines and 10–13 rays; anal fin with 5–7 spines and 8–9 rays; first bar on side of body, not "Y" shaped, usually not well marked; opercle without a black blotch on the upper half; small pale blue spots on soft dorsal rays and caudal fin ..... *Amphilophus diquis* (Figure 3A)

48 Premaxillaries extremely protractile; tail forked; body color silvery (Gerreidae) 49

48′ Premaxillaries slightly or non protractile; tail emarginate or truncate; body color variable 51

49 Body rhomboidal (depth about 50% of standard length); preopercle finely serrated; no stripes or bars ..... *Diapterus peruvianus* (Figure 3K)

49′ Body an elongate oval (depth 37–45% of standard length); preopercle smooth; with or without stripes or bars 50

50 Lateral-line scales 44–48; second anal spine shorter than depth of caudal fin base; no faint dark bars on side; spiny dorsal fin with grey base, white center, and wide black tip *Eucinostomus currani* (Figure 3L)

50′ Lateral-line scales 39–44; second anal spine longer than depth of caudal fin base; 8 faint dark bars on side; spiny dorsal fin transparent to yellowish ..... *Gerres simillimus* (Figure 3M)

51 Dorsal fin continuous (Labridae), with 8–9 spines and 11 rays; anal fin rays 12–13; enlarged canine teeth at front of both jaws (1 pair above, 2 pairs below), a canine at rear of upper jaws; lateral line with 27–28 pored scales ..... *Halichoeres aestuaricola* (Figure 4J)

51′ Dorsal fin continuous or with a shallow notch, with 10–13 spines and 12–14 rays; anal fin rays 7-8 52

52 Snout, below eye and lower jaw scaled; vomer without teeth; jaw teeth usually of same size (Haemulidae); dorsal fin with 12–13 spines and 12 rays, notched between the spinous and soft parts ..... *Pomadasys bayanus* (Figure 4G)

52′ Snout, below eye and lower jaw without scales; vomer with teeth, often small; some jaw teeth usually enlarged to form canines (Lutjanidae); dorsal fin with 10 spines and 14 rays, moderately notched between spinous and soft parts 53

53 Vomerine tooth patch anchor shaped, front curved or pointed; scale rows on upper back parallel to lateral line; soft dorsal and anal with angular ends;

body color rosy red anteriorly becoming bright yellow to orange over most of body; fins mainly yellow or orange; a blue horizontal streak below eye ..... *Lutjanus argentiventris* (Figure 4L)

53′ Vomerine tooth patch crescent shaped; scale rows on upper back rising obliquely above lateral line; soft dorsal and anal with rounded ends; tail with straight edge; body color dark olive brown to copper red on back and sides, becoming silvery white on lower sides; juveniles and adults with 8–9 dusky brownish bars on upper half, these sometimes obscure in large fish, which have dark fins ..... *Lutjanus novemfasciatus* (Figure 4M)

DISCUSSION

The total diversity of fish species in the Tusubres River Basin (54 species) represents 21.6% of the total diversity of native inland water fishes in the country (250 species) (Angulo et al. 2013). Taking into consideration the relatively small area of the basin, this number can be considered relatively high, with about 6.5 species/100 km² vs. about 0.5 species/100 km² on average for the country.

On the basis of Angulo et al. (2013), this basin ranks seventh in the country in terms of total number of species; from a total of 19 basins, the Tusubres River Basin is surpassed only by the Tortuguero (115 species), the Térraba (88 species), the Parismina (83 species), the Matina (75 species), the Sixaola (62 species), and the Sarapiquí (60 species) river basins. It is notable that most of these basins (5) are located on the Atlantic versant and only the Térraba River Basin is located on the Pacific versant. In addition, the Tusubres River Basin includes about 27.9% of the total diversity of inland water fishes in the Pacific versant of the country (Alpírez 1985; Angulo et al. 2013). Its geographical position, at the transition between two ichthyofaunal areas of endemism (Matamoros et al. 2014), and its environmental heterogeneity (Rojas 2011) could explain the relatively high diversity of fish species in this basin.

In general terms, the diversity and composition of the fish assemblage within the basin increased from upstream to downstream sites. Downstream sites were dominated by peripheral species of the order Perciformes, including families such as Eleotridae, Gobiidae, Gerreidae and Centropomidae, whereas upstream sites were dominated by primary and secondary species of the families Characidae (Characiformes), Cichlidae (Perciformes) and Poeciliidae (Cyprinodontiformes). As noted by Bussing (1998), Espinoza (2007), and Rojas and Rodríguez (2008), these differences in the assemblage composition largely reflect local differences in environmental conditions among sampled sites. In general terms this pattern corresponds to that observed in neighboring basins, Térraba for example (Rojas and Rodríguez 2008), as well as in the rest of the country (Bussing 1998). The dominance of peripheral species, in proportion to the total number of species, also is in accordance with that reported in the literature for Costa Rican inland waters in general (Bussing 1998; Angulo et al. 2013).

Localities 6, 11 and 12 showed very low diversity values (2–3 species, mean=2.33). This can be explained by the presence of several natural and/or artificial barriers (e.g., waterfalls or small dams) that limit the movement upstream of several species and/or by difficulties during the sampling (e.g., inadequate climatic conditions and/or problems or limitations with the use of some specific sampling gears). These localities were included in this work because in some of them, despite of these limitations, some uncommon and/or interesting species were recorded (e.g., *Pterobrycon myrnae* Bussing 1974, and *Hyphessobrycon savagei* Bussing 1967, Characidae; *Gymnotus maculosus*; and *Cynodonichthys isthmensis* (Garman 1895), Rivulidae). It is feasible that a more extensive and detailed sampling in these localities could result in higher values of fish diversity.

On the basis of Bussing (1987, 1998) and Angulo et al. (2013), two species (*Caranx sexfasciatus*, and *Opisthonema libertate*) are considered new records for Costa Rican inland waters. These peripheral species had already been recorded in coastal environments on the Pacific coast of the country (Bussing and López 2009); however, the present record is the first from inland waters.

Additionally, two primary freshwater species, *Gymnotus maculosus* and *Lebiasina boruca*, were found to have expanded distributional ranges. The previously known distribution of *G. maculosus* in the Pacific versant is between the San Nicolas River Basin (Chiapas, Mexico) and the Bebedero River Basin (Puntarenas, Costa Rica); the present record represents a southeastern range extension of about 85 km (straight-line distance). On the other hand, the previously known distribution of *L. boruca,* a species endemic to Costa Rica, is between the Térraba River Basin and the Coto River Basin (Puntarenas, Costa Rica); the present record represents a northwestern range extension of about 75 km (straight-line distance). Probably both species are residents in this area and likely remained undetected due to their rarity (only a few specimens (2–4) were observed and captured during this inventory), habitat specificity (only found in small creeks, where the current is of low or moderate velocity with abundant riparian and submerged vegetation (Bussing 1998)), and lack of prior targeted sampling (Bussing 1998).

By providing up-to-date knowledge on their diversity and distribution patterns we hope that the results of this investigation provide a useful framework for future biogeographic work on fishes from this area. This work is also aimed at aiding biologists, non-governmental

organizations and governmental agencies in establishing conservation actions, and in the promoting of the sustainable use of the fishes in the basin.

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