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Source: Copeia, 2011(1):93-102. 2011.
Published By: The American Society of Ichthyologists and Herpetologists
DOI: http://dx.doi.org/10.1643/CI-09-123
URL: http://www.bioone.org/doi/full/10.1643/CI-09-123

The Delta Mudsucker, *Gillichthys detrusus*, a Valid Species (Teleostei: Gobiidae) Endemic to the Colorado River Delta, Northernmost Gulf of California, Mexico

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Substantial genetic and subtle morphological characters document that the Delta Mudsucker or chupalodo delta, *Gillichthys detrusus* Gilbert and Scofield, 1898, family Gobiidae, is a valid species separate from its widespread sister species, the Longjaw Mudsucker, *G. mirabilis* Cooper, 1864. This species was erroneously placed in the synonymy of *G. mirabilis* in 1907 and has since remained unrecognized until this study. The Delta Mudsucker is restricted to a narrow zone of tidally influenced channels of the lowermost Colorado River and adjacent to the mouth of the river within its delta. It is the second fish species endemic to the river's delta in Mexico's Reserva de la Biósfera del Alto Golfo de California y Delta del Río Colorado (Upper Gulf of California and Colorado River Delta Biosphere Reserve). This study underscores the importance of continued reassessment of baseline and cryptic biodiversity, especially in habitats where initial assessment was scant prior to extensive anthropogenic influence.

Caracteres sustancial de genética y caracteres morfológicas sutiles sustentan que el chupalodo delta, *Gillichthys detrusus* Gilbert y Scofield, 1898, familia Gobiidae, es una especie válida, separada de su especie hermana de amplia distribución, el chupalodo grande, *G. mirabilis* Cooper, 1864. Esta especie fue erróneamente colocada en la sinonimia de *G. mirabilis* en 1907 y ha permanecida sin reconocimiento desde entonces hasta este estudio. El chupalodo delta está restringido a una zona angosta, influenciada por la marea, de la parte más baja del delta del Río Colorado en la parte más alto del Golfo de California, y es la segunda especie de pez endémica al delta dentro de la Reserva de la Biosfera del Alto Golfo de California y Delta del Río Colorado. Este estudio subraya la importancia de la revaloración continua de la biodiversidad base y críptica, especialmente en hábitats donde la evaluación inicial fue escasa antes de una influencia antropogénica severa.

RECENT comprehensive sampling and genetic characterization of mudsucker goby populations, genus *Gillichthys*, disclosed a distinctive population in the lowermost Colorado River and its estuary in the uppermost Gulf of California in northwestern Mexico. Morphologically these specimens closely resembled *Gillichthys detrusus* as described by Gilbert and Scofield (1898) from the same area. However, *G. detrusus* had long been considered a synonym of the widespread Longjaw Mudsucker, chupalodo grande, *Gillichthys mirabilis* Cooper, 1864, originally described from southern California. Examination of these new specimens and much of the original type materials revealed subtle morphological differences in addition to significant mitochondrial and nuclear gene sequence divergence justifying recognition of this poorly known species and its resurrection from the synonymy of *G. mirabilis*. We propose the common names Delta Mudsucker and chupalodo delta (Spanish) for this very narrowly distributed goby. Despite historically reduced freshwater input to the delta and its estuary (Rowell et al., 2008; Minckley and Marsh, 2009), this species will hopefully persist within the protection of the Core Area of the Reserva de la Biosfera del Alto Golfo de California y Delta del Rio Colorado (Upper Gulf of California and Colorado River Delta Biosphere Reserve) established by the Mexican government in 1993 (Hastings and Findley, 2007). It joins the Delta Silverside, or pejerrey delta, *Colpichthys hubbsi*, described by Crabtree (1989), as one of only two fish species entirely restricted to the Biosphere Reserve (Hastings and Findley, 2007). The restriction of the Delta Mudsucker to a small, relatively inaccessible, and poorly sampled geographic area, in addition to a general resemblance to its widespread congener, *G. mirabilis*, left it largely unrecognized until now.

DNA sequence analyses of the mitochondrial control region (i.e., D-loop) of recently collected specimens of *Gillichthys* spp. (California and Mexico) provided our first indication that the original description of *G. detrusus* might be valid. Results from additional sequencing of cytochrome *b* and the first intron of the S7 ribosomal protein coding gene, as well as morphometric and meristic data, support the species status of *G. detrusus*.

MATERIALS AND METHODS

Specimens of species within the genus *Gillichthys* were collected by seine from esteros and coastal lagoons on both sides of the Gulf of California, the outer coast of the Baja California peninsula, in the Colorado River delta, and the coast of California. Collected individuals were immediately placed in 95% ethanol and stored at −20°C (upon returning to the laboratory) for subsequent genetic and morphological analyses. Sampling localities for the two recent

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Submitted: 7 July 2009. Accepted: 29 October 2010. Associate Editor: D. Buth.
 DOI: 10.1643/CI-09-123

Fig. 1. Southern portion of the Colorado River delta showing the type locality and two recent collection localities of *Gillichthys detrusus* (modified from http://maps.google.com). Type locality at "Horseshoe Bend" in 1890 (Gilbert and Scofield, 1898) is approximated based on the 1908 USGS map of the region (Steve Nelson, pers. comm.). This locality is no longer part of the river due to eastward channel migration. The two recent collections are from near the former site of the boat landing, "Port Elizabeth," off the lower main channel of the river, and adjacent to the shrimp farm at Estero Santa Clara on the eastern edge of the delta (geographic coordinates given in Table 1).

collections of *G. detrusus* plus the type locality are shown in Figure 1. Specimens used in the molecular analyses were coded by species and locality (Table 1), individually numbered, and deposited (see additional material below for details of numbering and deposition) in Mexico's National Fish Collection (Colección Nacional de Peces, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, México D.F. [IBUNAM-P]) and the Natural History Museum of Los Angeles County (LACM). Additional museum materials were examined, including the syntypic series of both *G. detrusus* (USNM 48127) and *G. mirabilis* (USNM 5229), a large series of ''cotypes'' collected with the USNM ''types'' of *G. detrusus* (CAS 105432 and 103836, formerly SU 5432 and 3836, respectively), and several lots of *G. mirabilis* and *G. seta* from archived fish collections at UCLA, LACM, and CAS, including two additional series of *G. detrusus* not previously recognized. Institutional abbreviations are as listed at http://ww.asih.org/node/204, except IBUNAM-P given above.

Table 1. Localities for Recently Collected Specimens of *Gillichthys* from Estuaries in the States of California (CA), Baja California (BC), Baja California Sur (BCS), and Sonora (SO). Bold indicates sample localities used for morphometrics and meristics; * indicates localities used for genetic sampling. (For Estero Percebú, "c" is used in "PCBc" to distinguish multiple temporal collections from the same site. This also applies to "b" in samples "GmiGNGb1 and 2" and "GmiPCBb1" in Fig. 2). Coordinates were recorded with a hand-held GPS unit.

Locality	Abbreviation	Latitude (N)	Longitude (W)
Santa Barbara, CA*	USB	34°24.56′	119°50.70′
Ballona Lagoon, CA*	BNA	33°57.77′	118°26.75′
Punta Banda, BC*	BAN	31°45.98′	116°36.68′
San Quintín, BC*	QTN	30°25.92′	116°01.01′
Guerrero Negro, BCS*	GNG	28°01.30′	114°06.88′
San Ignacio, BCS*	IGN	26°49.12′	113°10.89′
Las Gallinitas, BCS*	GAL	24°33.02′	111°44.20′
El Mojón, BCS	MOJ	27°01.42′	112°00.62′
La Palmita, BC*	PAL	28°06.56′	112°48.68′
Las Ánimas, BC	ANI	28°47.86′	113°20.89′
La Gringa, BC*	GRI	29°02.38′	113°32.46′
Estero Percebú, BC	PCBc	30°47.74′	114°42.21′
Estero Segundo, BC*	SGU	31°15.36′	114°53.01′
Horseshoe Bend, BC	N/A (see Fig. 1)	—	—
"Port Elizabeth", SO*	ELZ	31°49.41′	114°49.57′
"Shrimp farm", SO*	SF	31°46.60′	114°34.63′
Estero La Pinta, SO*	ELP	31°15.90′	113°13.75′
"Gated estero", SO*	GE	30°57.35′	113°05.57′
Bahía Kino, SO*	KIN	28°47.50′	111°54.54′
Estero El Rancho, SO	RCH	27°58.21′	110°52.19′

Molecular procedures.—Muscle tissue was dissected from the caudal peduncle for DNA extraction using the DNeasy tissue extraction kit (Qiagen, Inc., Valencia, CA). The mitochondrial control region (D-loop) was amplified by polymerase chain reaction (PCR) using primers CRA and CRM (Lee et al., 1995). Reaction conditions consisted of an initial denaturation at 94°C for 2 min, followed by 40 thermal cycles of denaturation (95°C for 30 sec), annealing (52°C for 30 sec), and extension (68°C for 90 sec), with a final extension step at 68°C for 10 min. For cytochrome *b*, the following custom primers were designed for PCR amplification: CbGobF 5′–GCNTGATGRAACTTTGGGTCCC–3′ and CbGobR 5′–CCGGYTTACAAGACCGGCGCTC–3′. Reaction conditions were the same as above, with the exception of annealing temperature (59°C) and extension time (60 sec). The first intron of the S7 ribosomal protein-coding gene was amplified with primers S7RPEX1F and S7RPEX2R from Chow and Hazama (1998), using their reported reaction conditions. All PCR products were visualized on a 1.5% agarose gel to check for single bands of expected size, cleaned with the Wizard SV Gel and PCR Clean-Up System (Promega, Madison, WI), cycle sequenced with BigDye Terminator v3.1, and submitted to the UCLA GenoSeq core facility for capillary electrophoresis. All sequences were

Table 2. Raw Measurements (in mm) of Selected *Gillichthys detrusus* (Gde) and *G. mirabilis* (Gmi) Specimens. Locality abbreviations are described in Table 1. Bold indicates *G. detrusus* paralectotypes (USNM 394876); * indicates lectotype (USNM 48127). All other specimens have been deposited at IBUNAM-P and LACM (see Material Examined—Additional material). SL = standard length; HL = head length; SnoL = snout length; HW = head width; HD1 = head depth 1; HD2 = head depth 2; IWf = interorbital width, fleshy; IWb = interorbital width, bony; EL = eye length; UJL = upper jaw length (see Materials and Methods for description of each measurement).

Specimen	Sex	SL	HL	SnoL	HW	HD1	HD2	IWf	IWb	EL	UJL
Gde1	F	82.7	26.4	5.3	14.3	12.5	7.9	6.1	3.3	2.7	18.3
Gde2	F	76.5	24.0	5.4	14.5	12.5	8.0	4.5	2.2	3.2	16.8
Gde3*	M	93.5	29.5	7.0	19.1	15.0	10.4	7.2	3.9	3.2	25.0
Gde4	F	80.2	25.0	5.7	14.6	12.2	9.1	4.7	3.4	3.1	17.0
GdeELZ1	F	79.3	24.3	4.8	14.2	12.3	8.5	4.9	2.8	4.4	17.1
GdeELZ2	M	86.5	28.7	5.5	15.9	14.5	10.6	5.2	3.2	4.5	26.3
GdeELZ3	F	83.3	25.3	5.3	15.4	13.2	10.3	4.6	2.9	—	18.8
GdeELZ4	F	80.0	26.7	6.7	13.8	13.1	9.7	5.4	2.7	3.8	19.5
GdeELZ5	F?	62.4	19.9	4.0	11.3	8.7	6.5	2.8	2.3	2.5	13.6
GdeELZ6	F?	63.0	20.0	4.1	11.6	9.8	6.7	3.3	2.2	3.3	13.5
GdeELZ7	F?	76.3	23.9	5.0	12.7	12.1	8.0	4.5	2.6	4.0	17.3
GdeELZ8	F	57.4	17.7	3.4	9.3	7.9	4.9	3.0	1.5	2.9	11.8
GdeSF1	F	76.7	23.1	5.3	14.9	13.4	10.2	4.5	3.0	4.1	16.8
GdeSF2	F?	74.5	23.8	5.1	13.3	11.9	7.7	4.1	2.6	3.9	17.7
GdeSF3	F	63.7	18.9	4.7	11.9	9.7	7.1	3.4	1.9	3.8	13.1
GdeSF4	F?	63.0	18.9	3.9	11.7	10.4	8.6	2.5	1.5	3.6	13.1
GmiPCBc0	M	83.8	26.1	6.0	15.0	12.4	10.0	4.1	2.0	5.4	21.6
GmiPCBc1	F	102.8	32.6	7.3	19.5	17.1	11.1	5.5	3.0	6.8	29.0
GmiPCBc2	F	101.0	33.5	6.5	19.7	17.3	12.4	5.7	3.7	7.6	27.9
GmiPCBc3	M	45.6	14.2	2.6	7.7	6.8	5.1	1.2	1.0	3.4	8.5
GmiRCH1	M	78.0	26.5	6.0	16.6	14.8	11.9	4.6	2.6	5.6	25.1
GmiANI7	F?	87.5	28.3	5.2	16.3	13.4	10.2	5.3	3.2	4.8	22.1
GmiANI8	F?	105.8	36.1	9.6	22.2	18.5	14.7	8.0	4.2	5.8	33.9
GmiANI9	M	116.0	40.3	9.5	23.9	19.7	15.6	8.2	4.3	7.4	43.5
GmiANI10	F	75.4	24.3	4.3	15.0	12.9	9.5	4.1	2.1	4.5	20.5
GmiMOJ4	F?	72.2	22.4	5.3	15.3	13.2	9.5	4.9	2.4	4.1	18.2
GmiMOJ5	F?	54.8	16.6	3.9	11.0	8.6	6.2	2.3	1.1	3.8	12.6
GmiMOJ7	F?	68.5	20.8	4.4	15.0	11.4	8.1	3.0	1.5	4.8	15.3
GmiMOJ9	?	53.1	16.4	3.5	10.2	9.5	6.6	3.0	1.5	3.4	10.7
GmiMOJ10	M?	67.7	20.9	4.5	13.4	10.6	8.0	4.2	1.9	4.2	16.8
GmiBNA1	F?	88.4	26.3	6.1	17.9	16.5	11.6	5.9	3.3	4.8	21.6
GmiBNA2	F	107.0	34.0	7.8	24.9	19.7	11.2	5.1	3.7	5.6	28.1
GmiBNA3	F?	94.8	25.8	5.8	21.4	16.7	9.5	3.7	2.5	4.7	21.8
GmiBNA5	M?	87.6	27.4	4.7	16.6	15.4	10.4	3.8	2.6	5.4	23.2
GmiBNA7	F?	71.3	22.6	4.8	17.0	13.6	10.2	3.8	2.0	4.2	17.3
GmiBNA8	F	67.7	21.3	3.8	12.3	11.5	8.0	3.1	2.3	4.5	16.5

unambiguously aligned by eye, and GenBank accession numbers for all sequences used here are FJ861668–FJ861693 (cyt*b*) and GQ368426–GQ368451 (S7 intron).

Phylogenetic methods.—Cytochrome *b* and S7 intron sequences were used for phylogenetic analysis of the genus *Gillichthys*. Bayesian phylogenies were reconstructed in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), using the general time reversible plus proportion of invariant sites model of sequence evolution (GTR+I), chosen by the Akaike Information Criterion (AIC) method in MrModelTest (Posada and Crandall, 1998). Likelihood bootstrap values were calculated with 100 replicates in GARLI v0.95 using the Tamura Nei+I (TrN+I) model as chosen by jModelTest using both AIC and Bayesian Information Criterion methods (Guindon and Gascuel, 2003; Posada, 2008). Fixed differences in the S7 intron were counted by eye in MacClade v4.08 (Maddison and Maddison, 2005). The basal placement *G. seta* was determined by a phylogenetic analysis where related genera (eastern Pacific genera *Quietula*, *Ilypnus, Eucyclogobius, Clevelandia, Evermannia, Lepidogobius*, and the western Pacific genus *Gymnogobius*) served as outgroup taxa (Ellingson and Jacobs, unpubl.). Divergence time estimation in this analysis was performed in BEAST v1.4.7 (Drummond and Rambaut, 2007), utilizing the biogeographic calibration reported by Sota et al. (2005).

Morphology.—Counts and measurements were taken following Hubbs and Lagler (2004), except for some cephalic measurements (see below). Measurements were taken with dial calipers to the nearest tenth of a millimeter. Vertebral counts and some median fin ray counts were taken from radiographs. On some frozen and alcohol-preserved specimens the skin was dissected from the pectoral-fin base to facilitate counting small marginal rays. The nine measurements taken (Table 2) are defined as follows: HL = head length, from snout tip to attachment of upper opercular

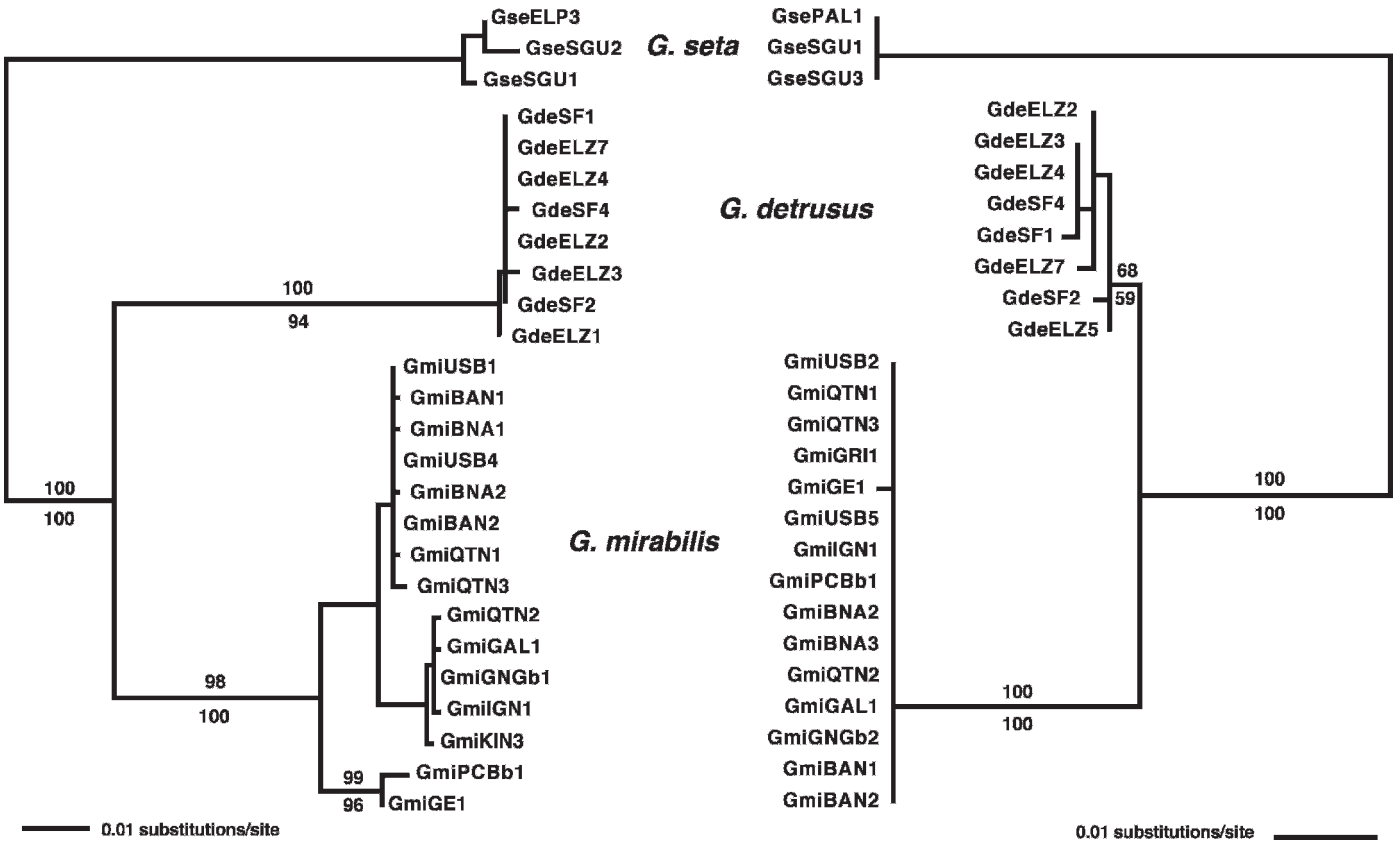

Fig. 2. Phylogenetic relationships within the genus *Gillichthys*. Both trees were created in MrBayes (right: first intron of S7 ribosomal protein gene, left: cytochrome *b*), with posterior probabilities shown above branches and maximum likelihood bootstrap values (100 replicates calculated in GARLI) shown below branches. Specimen locality abbreviations follow Table 1.

membrane on left side; SnoL = snout length, snout tip to anterior fleshy margin of left eye; HW = head width, transverse measurement, distance between pre-opercular margins at lateral midline of head; HD1 = head depth 1, vertical measurement at level of pre-opercular margins at occiput; HD2 = head depth 2, vertical measurement from midline between the eyes to throat (gular) area below; IWf = interorbital width, fleshy; IWb = interorbital width, bony; EL = eye length, fleshy left eye; UJL = upper jaw length, tip of snout to tip of maxillary, left side. Measurements were taken from similar sized fish, where SL of *G. detrusus* ranged from 57.4–93.5 mm ($\bar{x}$ = 74.9 mm, n = 16) and a range in *G. mirabilis* of 45.6–116.0 mm ($\bar{x}$ = 81.5 mm, n = 20).

A discriminant function analysis (DFA) was conducted as a means to identify which of the above measurements systematically discriminated between specimens of *Gillichthys mirabilis* and *G. detrusus*. The nine measured variables were standardized by the expedient of division by standard length, and analyzed in a stepwise discriminant analysis using in SPSS-11. The results of the phylogenetic analysis provided the premise that there are two distinct species defined *a priori* appropriate for this subsequent DFA.

RESULTS

Molecular systematics.—Sequencing of mitochondrial cytochrome *b* (cyt*b*) and the first intron of the nuclear S7 ribosomal protein gene provided convincing genetic evidence of reproductive isolation and divergence between populations of *G. mirabilis* from the upper Gulf of California and *G. detrusus* in the Colorado River delta. For the *G. detrusus* S7 intron, sequence analysis revealed 14 fixed nucleotide substitutions and two distinguishing indels (1-bp and 4-bp) out of 654 unambiguously aligned sites, despite no variation within our samples of *G. mirabilis*. For the protein-coding cyt*b*, there were expectedly no indels, but fixed substitutions between the two species were present at 70 of 989 sites. Phylogenetic reconstruction shows strong support for reciprocal monophyly between *G. mirabilis* and *G. detrusus* in nDNA sequences (Fig. 2, right), and is supported by the same results in mtDNA (Fig. 2, left).

Morphology.—The genus *Gillichthys* contains three superficially similar species, distinguished by several minor morphologic differences. Specimens of *G. seta* have the first (and occasionally second) uppermost pectoral-fin ray free from the fin membrane for the posterior one-quarter to one-half of its length, whereas the other two species have all pectoral-fin rays fully joined by membrane.

The most obvious difference among the species of *Gillichthys* is the dorsal and lateral profile of the head. As in *G. seta* (Barlow, 1961), the head of *G. detrusus* is more depressed (Fig. 3C; Gilbert and Scofield, 1898:pl. 38), whereas the head of *G. mirabilis* is deeper and more rounded (Fig. 3D). Thus, in profile, the head of *G. mirabilis* has a broadly rounded snout and convex dorsal outline, whereas *G. seta* and *G. detrusus* have a flat or nearly flat dorsal outline above the mouth. At the snout and anterior to the eye in *G. detrusus*, this flat top drops downward abruptly (almost vertically) to the essentially terminal and horizontal mouth (Fig. 3C). In *G. seta* this flat preocular cephalic surface extends anteriorly all the way to the upper jaw median since

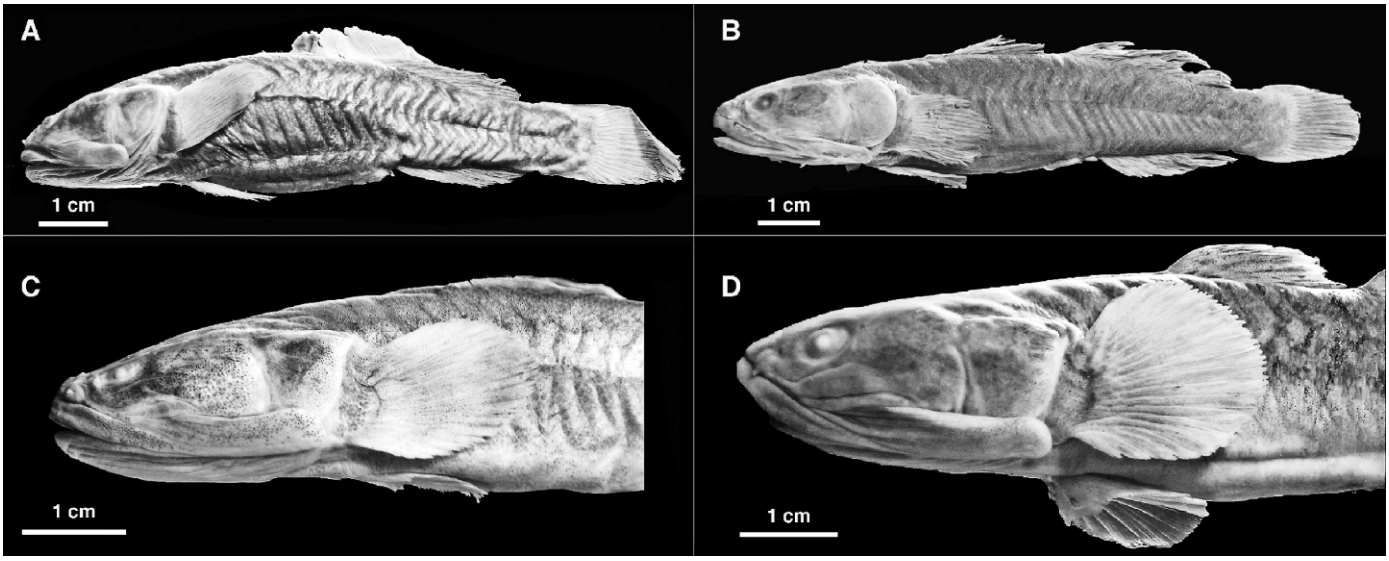

Fig. 3. Types and recently collected specimens of species of *Gillichthys*: (A) lectotype of *G. detrusus*, adult female, USNM 48127, ''Horseshoe Bend,'' MX; (B) syntype of *G. mirabilis*, adult male, USNM 5229, San Diego, CA, USA; (C) *G. detrusus*, adult male, GdeELZ2, ''Port Elizabeth,'' MX; (D) *G. mirabilis*, adult male, LACM 56805-1, Devereaux Slough, CA, USA.

the mouth is slightly upturned. Thus, the head of *G. mirabilis* appears largely conical (or only slightly depressed), that of *G. detrusus* is notably depressed and narrowly and abruptly rounded at the snout tip, and that of *G. seta* is even more depressed, appearing flat and incipiently spatulate with the mouth turned slightly upward. Two variables associated with the greater relative flatness of the head in *G. detrusus,* greater head width (HW) and larger eye length (EL), are the primary measurement variables that effectively differentiate *G. detrusus* and *G. mirabilis* in the discriminant function analysis (Fig. 4). Thus, Gilbert and Scofield's (1898) specific epithet *detrusus*, meaning ''depressed'' in Latin, is informative, and the discriminant function analysis supports the separation of these taxa consistent with the molecular phylogenetic results (Fig. 2). The discriminant function correctly attributed 33 of 35 specimens to species. This morphometric effort should be regarded as preliminary. Given the extensive range of *G. mirabilis* and previous arguments regarding the paedomorphic origin of *G. seta* (Barlow, 1961; Huang and Bernardi, 2001), more broadly geographic and ontogenetic morphometric work using more samples, measurements, and a more sophisticated analytic approach across all three species of *Gillichthys* appears merited.

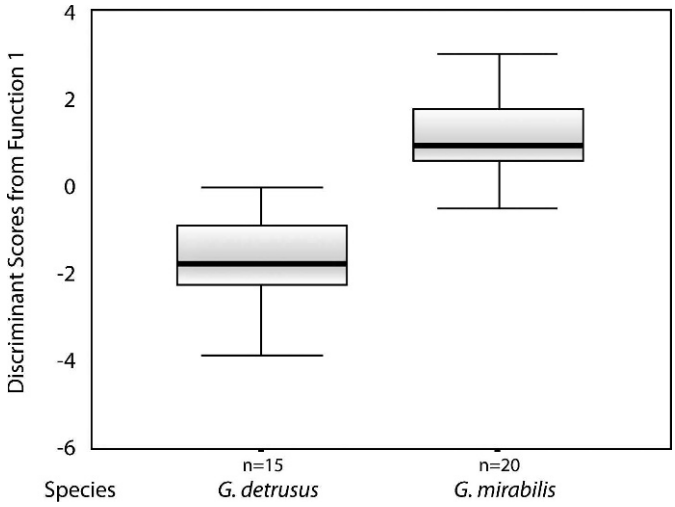

Fig. 4. Box-plots illustrating difference in mean discriminant scores between *Gillichthys detrusus* and *G. mirabilis*.

Another diagnostic feature noted by Gilbert and Scofield (1898), and confirmed by us, is the greater distance between the dorsal-fin bases; this distance is about one-half the length of the first-dorsal base in *G. detrusus*, versus one-third or less the length of the first-dorsal base in *G. mirabilis and G. seta*. The depressed first dorsal fin falls distinctly short of the second dorsal-fin origin in *G. detrusus,* versus reaching or nearly reaching this point in *G. mirabilis*. This character has not been appreciated because careful examination is required to determine the posterior limit of the first dorsal base as distinct from the posterior extent of the depressed fin, an area where the fin membranes are often torn.

The Delta Mudsucker is also pallid in coloration. Freshly caught specimens were pale olive or gray overall, without the dark irregular patterning on the body usually seen in the other two species. Later, after being frozen in ethyl alcohol, these specimens remained pale with the only pigment markings being a light dusting of minute, concentrated melanophores on the body and fins. The CAS specimens clearly show this fine dusting of concentrated melanophores along the dorsal one-third of the body in contrast to the expanded melanophores typical of *G. mirabilis* specimens of the same vintage. The pectoral fins in these CAS specimens and our fresh specimens of *G. detrusus* are lightly pigmented dorsally, but have only a few melanophores, or lack them completely, on the ventral one-half to one-third of the fin, whereas the fin is strongly pigmented throughout in *G. mirabilis* and *G. seta*. Gilbert and Scofield (1898) also remarked on the ''very pale olive'' coloration of their specimens when fresh, and Barlow (1961) clearly illustrated the more intense coloration of *G. mirabilis* and *G. seta*. Our freshly collected specimens of *G. detrusus* were all adults. However, the CAS sample includes a range of sizes (116 specimens, 18–111 mm SL) and small individuals have a uniform dusting of fine melanophores along the dorsal one-third of the body from head to tail, much as the adults from

other samples do. There is no sign of the distinct unpigmented area at the caudal-fin base typical of small juvenile *G. mirabilis* (Barlow, 1961:fig. 4, top).

Meristics.—With the exception of pectoral-fin ray counts, our data and Barlow's (1961, 1963) show that *G. mirabilis* and *G. detrusus* (to the extent that he examined material of *G. detrusus*) are very similar in meristics and differ strongly from *G. seta*. The flexible first dorsal-fin spines almost always number six in the three species, and second dorsal-fin rays number 12 or 13 in *G. mirabilis* and *G. detrusus* (the last ray, split from its base, counted as one). These two species usually have 12 anal-fin elements, namely an anterior flexible spine and 11 soft rays (occasionally 10 or 12). In contrast, *G. seta* usually has 11 second-dorsal-fin rays (occasionally 10 or 12) and nine or ten anal elements. We counted pectoral-fin rays of recently collected *G. detrusus* (12 specimens), the lectotype (USNM 48127), the three largest paralectotypes (USNM 394876), as well as CAS 103836 (1 specimen) and CAS 105432 (8 specimens). Counts (both fins) averaged higher in *G. detrusus* than in the other two species: *G. detrusus* had 21(7), 22(34), or 23(9) rays ($\bar{x}$ = 22.05, SD 0.64; *G. mirabilis* had 19(1), 20(17), 21(22), 22(2), or 23(2) rays ($\bar{x}$ = 20.6, SD 0.63); *G. seta* had 21(14) or 22(6) rays ($\bar{x}$ = 21.3, SD 0.47). These averages are highly significantly different: t = 10.408, two-tailed $P < 0.0001$ for comparison of *G. detrusus* and *G. mirabilis*; and t = 4.6521, $P < 0.0001$ for comparison of *G. detrusus* and *G. seta*.

The small, imbedded nature of the scales in species of *Gillichthys* makes reliable scale counts difficult. Although Barlow (1961) used the presence/absence of scales on the midline of the nape to distinguish *G. seta* (in which they are almost always absent) from his *G. mirabilis* (*sensu lato*), that character cannot distinguish all individuals of *G. detrusus* from *G. mirabilis* (both usually have nape scales and they are non-overlapping in *G. detrusus*). Like other species of *Gillichthys*, small juvenile *G. detrusus* have prominent overlapping denticulate or crenulate scales, most prominent posteriorly, and these become progressively imbedded and lose their crenulation with age and growth. Vertebral counts are similar, varying between 30 and 32 total vertebrae (including the urostyle counted as one vertebra) in *G. detrusus* versus 30 to 33 in *G. mirabilis*, with a usual total vertebral count of 32 for both. *Gillichthys detrusus* consistently has 14 or 15 precaudal (abdominal) vertebrae, whereas some populations of *G. mirabilis* from the mid-Gulf of California consistently have 16 (ANI, MOJ; see Table 1 for locality abbreviations). Other populations of *G. mirabilis* from the northern Gulf of California (PCBc), central Gulf of California (RCH), and the coast of southern California (BNA) have counts similar to *G. detrusus*. Clothier (1950) reported 32 total vertebrae in 15 of 17 specimens of *G. mirabilis* from Huntington Beach and Seal Beach in southern California, and 31 and 33, respectively, in his other two specimens. Gill-raker counts are slightly higher in *G. detrusus* compared to *G. mirabilis*; in *G. detrusus* the counts were four or five on the upper limb and 12 to 14 on the lower limb of the first gill arch (CAS 103836, 105432 [9 specs.]; USNM 48127 [4 specs.]). Barlow (1961) gave a total gill-raker count with ranges of 2–4 + 10–12 for *G. mirabilis*.

DISCUSSION

Gillichthys detrusus was described by Gilbert and Scofield (1898) from specimens collected by C. H. Gilbert and A. B. Alexander in late April and early May of 1890 in the ''Horseshoe Bend'' of the lower Colorado River below ''Lerdo'' (Gilbert and Scofield, 1898; Jordan and Evermann, 1898). Lerdo Landing, now long-abandoned, was near Colonia Lerdo on the Sonora side of the river in northwestern Mexico and approximately 97 river miles (155 km) below Fort Yuma, Arizona (Fig. 1; based on Lingenfelter, 1978:appendix C). The main channel of the river currently lies eastward, placing the type locality on dry land in the state of Baja California (Fig. 1). Gilbert and Scofield's description was accepted and paraphrased by Jordan and Evermann (1898:2251). Starks and Morris (1907), however, placed *G. detrusus* in the synonymy of the more widespread *G. mirabilis* based on mensural data on six specimens from a larger series, now labeled as ''cotypes'' from the former Stanford University Fish Collection (SU 5432, now CAS 105432).

Later, the name *G. detrusus* was confused in various ways. Hubbs (1921), Jordan et al. (1930), and Weisel (1947) used the name, but either considered it to represent all populations of *Gillichthys* in the Gulf of California, or were confused by specimens of the then undescribed *G. seta*, described by Ginsburg (1938) as *Lepidogobius seta*. It is clear from published (Ginsburg, 1945) and unpublished archived notes (Fish Division, USNM) that Ginsburg initially considered the nominal *G. detrusus* to apply to all populations of *Gillichthys* in the Gulf of California except his new species, *G. seta*. Later, he noted a difference in pectoral-fin ray counts between the types of *G. detrusus* and *G. mirabilis* and wrote ''the precise value of this difference remains to be determined by a study of large numbers of specimens including those from intermediate localities'' (Issac Ginsburg, unpublished MS on American gobies). Evans and Douglas (1950) identified several baitfish introductions from the Salton Sea and lower Colorado River in California as *G. detrusus*, calling them ''Gulf mudsucker.'' Carl Hubbs and Robert Miller (in Miller, 1952) reexamined this material and identified the specimens as ''*G. mirabilis*'' except for two fish from a pelican rookery at the southern end of the Salton Sea (SIO49-113). They believed these individuals might be *G. detrusus* based on Ginsburg's unpublished notes. These specimens examined by Hubbs at SIO were not retained, probably due to poor condition (H. J. Walker, SIO, pers. comm.). Hubbs (in Miller, 1952) believed white pelicans carried these specimens into California from Mexico. Miller (1952) included both *G. mirabilis* and *G.detrusus* in his baitfish key, using the difference in number of pectoral-fin rays that Ginsburg suggested as a potentially diagnostic character. Barlow (1961, 1963) exhaustively studied morphological variation in *G. mirabilis* and the northern Gulf of California endemic *G. seta,* now called the Shortjaw Mudsucker or chupalodo chico. He noted the description of *G. detrusus*, but considered his study material of *Gillichthys* (including Stanford material labeled as ''cotypes'' of *G. detrusus*) from upper Gulf of California localities to be *G. mirabilis*. He agreed with Starks and Morris (1907) and retained *G. detrusus* in the synonymy of *G. mirabilis,* an action paralleled by Follett (1961). Barlow (1961) noted that Carl Hubbs had earlier 'recognized' the nominal *G. detrusus* based on material of the then undescribed congener *G. seta*. *Gillichthys detrusus* has not been recognized by others since Barlow's studies (Hoese, 1995; Ruiz-Campos et al., 2000; Minckley, 2002; Nelson et al., 2004; Miller et al., 2005; Hastings and Findley, 2007; Minckley and Marsh, 2009).

Follett (1961) mentioned Hubbs as the source for a freshwater record of *G. mirabilis* in the Colorado River delta from the Rio Hardy tributary, just above ''Ponge [*sic*] de Abajo'' and one mile (1.6 km) down from the tide gauge, with no date given. This locality is in the delta and the fish could have been *G. detrusus*. Possibly they were the specimens of *Gillichthys* noted among a series of collections progressing down the Colorado River from Laguna Dam to tidewater and described by Evans and Douglas (1950) as near the head of tidewater below the mouth of the Rio Hardy. The two most likely repositories for specimens, SIO and the University of Michigan Museum of Zoology (UMMZ), have no records matching this locality (H. J. Walker [SIO], Douglas Nelson [UMMZ], pers. comm.).

Following the fourth edition of the International Code for Zoological Nomenclature (1999, Article 73.2.1), we considered archived museum material from 1890 collection of *G. detrusus* to be syntypes despite previous designations as ''types,'' ''paratypes,'' ''co-types,'' and even ''holotype'' by earlier authors and museum records. Gilbert and Scofield (1898) named USNM 48127 as ''type'' of *Gillichthys detrusus* currently consisting of 97 specimens (about 15 to 93.5 mm SL; see Fig. 1A for this largest specimen). Additional specimens from the same collections were labeled as ''cotypes'' in the Stanford collection, now in the California Academy of Sciences: CAS 105432 (SU 5432), 116 specimens, 18.1–111.0 mm SL; CAS 103836 (SU 3836), 1 specimen, 99.1 mm SL. This latter specimen has a metal tag with the word ''drawn'' embossed on it and is clearly the fish illustrated in Gilbert and Scofield (1898:plate 38). Additional material listed as ''paratypes'' by Eschmeyer (1998) as ''from Gilbert,'' are BMNH 1897.1.12.32–37, 6 specimens; MCZ 35909, 1 specimen ''from USNM 48127''; and NMW 31091, 1 specimen, for a grand total of 222 syntypes. However, only five specimens, 23.6–101.0 mm SL, are currently in the BMNH jar labeled ''*Gobius detrusus* types'', and no indication could be found to account for the absence of the sixth specimen (P. Campbell, BMNH, pers. comm., 10 August 2009). The MCZ 35909 specimen is listed as ''paratype'' in online museum records with attribution to Barlow (1961) and determination by ''D. Hoese'' in 1990. An additional specimen is listed on the website for the Swedish Museum of Natural History, also specifically designated as from ''USNM 48127,'' described as ''paratype,'' and cataloged as ''NHRM 10769, one specimen, discolored by a metal tag.'' Böhlke (1953) indicated USNM 48127 was the ''holotype'' for *G. detrusus,* but such had never been designated from the series of specimens. Eschmeyer (1998) noted the holotype should come from the USNM 48127 series if the species was identifiable. We examined all USNM and CAS material and relied on the literature, websites, and communications with collections staff for information on the few other syntypes distributed long ago. Most of the syntypes are small: USNM 48127 contains 93 specimens about 15–20 mm SL, plus four others 76.4–93.5 mm SL. The 93.5-mm adult female (Fig. 3A) is here selected as lectotype for *G. detrusus* and retains the original number USNM 48127. The remaining 96 paralectotypes have been re-cataloged as USNM 394876 (D. Pitassy and J. Williams, pers. comm.). Because all specimens were collected over a short time period at the same locality and were clearly used in the original description, we also designate the two CAS lots as paralectotypes. These two lots, CAS 105432 (116 specimens) and CAS 103836 (1 specimen), were both labeled as ''cotypes'' and called ''paratypes'' by Böhlke (1953). The few other specimens distributed to other institutions have not been examined and are not designated as paralectotypes at this time. Measurements for the USNM lectotype and the three larger paralectotypes are given in Table 2.

A syntype of *Gillichthys mirabilis* (USNM 5229; Fig. 3B) is part of Cooper's type series (Isaac Ginsburg, USNM website notes). It bears the same data given by Cooper (1864) for four specimens he noted as ''types'' and as catalog number 627 in the California State Collection. It is uncertain when, and how many, specimens were received by the USNM (J. Williams, USNM, pers. comm.). However, at least two specimens were received. USNM 5229 continues to reside at USNM, while another specimen, sent to the Muséum national d'Histoire naturelle in Paris in 1881, was reported as a ''syntype'' by Bauchot et al. (1991). Any specimens remaining in California probably were incorporated into the subsequent California Academy of Sciences and lost during the 1906 earthquake and fire in San Francisco. The type status of the two extant syntypes should await a detailed study of this widespread species, including the nominal synonyms *Gobius townsendi*, described by Eigenmann and Eigenmann (1889), and *Aprolepis barbarae*, described by Hubbs (1921), from San Diego and Carpenteria, California, respectively, both taxa based on juvenile specimens of *G. mirabilis* (Barlow, 1961).

Recognition of *Gillichthys detrusus* adds another species to the group of mostly temperate northeastern Pacific ''bay gobies'' (Dawson et al., 2002) first delineated by Ginsburg (1945, unpubl. notes, Fish Division, USNM) and expanded to include several western North Pacific genera by Birdsong et al. (1988). Thacker (2009) recently placed this ''bay goby'' group along with other goby taxa into a separate family Gobionellidae, a name whose application and usage may require further clarification. Within the ''bay goby'' group, *G. detrusus* is apparently unique in being very restricted in distribution to the tidal portions of the lower Colorado River channel and its immediate estuary. Molecular data confirm the presence of its congener, *G. mirabilis,* in nearby Estero Primero at the southwestern edge of the delta (Ellingson and Jacobs, unpubl.) and from the Puerto Peñasco area to the southeast (Huang and Bernardi, 2001). Molecularly confirmed samples of *G. seta* are found even closer, at Estero Segundo and from just south of the fishing town El Golfo de Santa Clara, at the southwestern and southeastern parts of the delta, respectively. Thus, *G. detrusus* lives in very close proximity to its congeners.

The three species of *Gillichthys* live in somewhat distinct habitats: *G. mirabilis* is usually found in marsh-top muddy channels in estuaries; *G. seta* in high intertidal pools and tidal rivulets of rocky and sandy shores; *G. detrusus* was found at low tide in deep channels produced by the 10 meter tidal amplitude in the Colorado River estuary, where fine, silty sediments and turbid conditions are pervasive. Recent collections of *G. detrusus* came from only two localities separated by about 25 km, and an additional 25 km away from the type locality, which is no longer tidal habitat. The ''Port Elizabeth'' locality was in a side channel of the Colorado River. Specimens from the ''Shrimp farm'' site came from a minor channel of what was once referred to as ''Santa Clara Slough'' or Estero Santa Clara, now bounded by a shrimp farm (Fig. 1). Estero Santa Clara forms the western margin of the delta and opens onto the larger estuary of the

Colorado River. Both localities are similar in their large tidal amplitude, channel depth, and fine sediments. The range of *G. detrusus* is remarkably narrow for a salt-tolerant taxon with unimpeded access to the marine realm; thus, it appears to be one of the most geographically restricted species of marine fishes on a continental coast.

The type series of *G. detrusus* contains three almost non-overlapping size classes of fish. In CAS 105432, 93 are 18.1–28.2, 15 are 31.0–50.0, and 8 are 74.3–111.1 mm SL. The lectotype/paralectotype series in the USNM consists of four fish from the largest class and 93 others in the smallest class. These groups probably represent three year-classes, suggesting spawning during the few months before the sampling period, April and May of 1890. Thus, reproduction likely occurred in the late winter–early spring season, a few months before the usual historic late spring–early summer highest flow period in the main river (Minckley and Marsh, 2009).

Gillichthys detrusus and *G. mirabilis* are sister taxa, and this split is relatively old (Bayesian methods estimate the divergence time to be approx. 5 my; Ellingson and Jacobs, unpubl.) and may correlate with the development of the Colorado River estuary following the opening of the Gulf of California. It may be that the three species of *Gillichthys* evolved in allopatry and only more recently came into close proximity in the northern Gulf of California. This tentative chronology, along with an analysis of *G. mirabilis* proper, will be the subject of forthcoming studies. While only two species of fishes, *G. detrusus* and the atherinopsid *Colpichthys hubbsi,* are restricted to the Reserva de la Biosfera del Alto Golfo de California y Delta del Rio Colorado, several other endemic marine fishes and invertebrates are present in the northern Gulf of California (Brusca et al., 2005; Brusca, 2010) and contribute to the northern Gulf's high level of marine endemism (Hubbs, 1961; Walker, 1961; Hastings and Robertson, 2001; Dawson et al., 2006; Hastings et al., 2010; Jacobs, unpubl.). Our continuing studies utilizing fine-grained genetic analysis of estuarine-restricted taxa should provide nuanced and detailed patterns of faunal evolution in this dynamic region.

KEY TO THE SPECIES OF *GILLICHTHYS*

1a. One (occasionally two) uppermost pectoral-fin rays free from the fin margin; total anal-fin elements 9 or 10; soft dorsal-fin rays 10–12 (usually 11); nape naked or rarely with a few scales; body usually darkly pigmented, with melanophores present even ventrally, where only the extreme midline and part of the chest lacks pigment ..... ***Gillichthys seta*** endemic to the upper Gulf of California

1b. Upper edge of pectoral fin continuous, with all small upper rays enclosed in a continuous membrane; total anal-fin elements usually 11 or 12; soft dorsal-fin rays usually 12 or 13; nape with a narrow strip of non-overlapping, imbedded scales; body usually pale on its ventral one-third to one-half 2

2a. Scaled space between dorsal-fin bases one-third or less the length of first dorsal-fin base; body and head mottled and blotched with stellate and expanded melanophores, specimens less than about 50 mm SL with distinct depigmented band on caudal peduncle in advance of caudal-fin base (sometimes accompanied by a small dark caudal spot on the posterior edge of this pale area); pectoral-fin rays usually 21 or less; eyes placed dorsolaterally but directed laterally ..... ***Gillichthys mirabilis*** widely distributed from northern California to the Gulf of California

2b. Scaled space between dorsal-fin bases about one-half the length of first dorsal-fin base; body overall very pale, all melanophores concentrated into very small spots scattered uniformly as a light peppering over dorsal one-third of body evident in specimens of all sizes; pectoral-fin rays usually 22 or more; eyes placed and directed dorsolaterally ..... ***Gillichthys detrusus*** Colorado River estuary

MATERIAL EXAMINED

Type material.—*Gillichthys detrusus,* lectotype, USNM 48127; paralectotypes, USNM 394876; CAS 105432 (ex. SU 5432); CAS 103836 (ex. SU 3836), data given above. *Gillichthys mirabilis*, syntype, USNM 5229, data given above.

Additional material.—Non-type material used in this study is listed here. Specimens collected for this study are identified throughout by a species/locality/individual specimen-number code where a species designation (Gde, Gmi, or Gse) is combined with a locality abbreviation and a sample number (e.g., GdeELZ1). These codes serve to trace specimen, taxon, and locality from tissue to DNA to data, as well as in the text and on the trees (Fig. 2). These codes are followed below by their respective museum catalog number. Table 1 gives localities sampled, locality abbreviations, latitude/longitude coordinates, and also indicates from which localities sampled specimens were selected for morphometric/meristic and/or genetic analyses. Table 2 presents morphometric data for selected specimens of *G. detrusus* and *G. mirabilis*. All localities are in northwestern Mexico or California, USA. Museum catalog number, locality, collection date, and names of collectors are given for specimens not appearing in Tables 1 and 2 [e.g., CAS 82502].

Gillichthys detrusus: GdeELZ1-8, IBUNAM-P 15708-1 to 8; GdeSF1-4, IBUNAM-P 15709-1 to 4; CAS 82502, Mexico, Baja California, Colorado River at the ''75-km ferry'', 12 March 1957, Kimsey, McCammon, and Hagy.
Gillichthys mirabilis: GmiUSB1-2 and 4-5, LACM 57117-1 to 4; GmiBNA1-3, 5, and 7–8, LACM 57116-1 to 6; GmiBAN1-2, IBUNAM-P 15717-1 to 2; GmiQTN1-3, IBUNAM-P 1715-1 to 3; GmiGNGb1-2, IBUNAM-P 15714-1 to 2; GmiIGN1, IBUNAM-P 15716-1; GmiGAL1, IBUNAM-P 15724-1; GmiMOJ4-5, 7, and 9–10, IBUNAM-P 15713-1 to 5; GmiANI7-10, IBUNAM-P 15712-1 to 4; GmiGRI1, IBUNAM-P 15723-1; GmiPCBc0-3, IBUNAM-P 15710-1 to 4; GmiGE1, IBUNAM-P 15722-1; GmiKIN3, IBUNAM-P 15721-1; GmiRCH1, IBUNAM-P 15711-1.
Gillichthys seta: GsePAL1, IBUNAM-P 15719-1; GseSGU1-3, IBUNAM-P 15718-1 to 3; GseELP3, DNA sample, Estero La Pinta, Sonora, courtesy of G. Bernardi (UCSC); UCLA W54-230, Sonora, Punta Pelícano, 8 mi. [12.8 km] W of Puerto Peñasco, 28 April 1954; LACM 48363-1 (=W50-193), Baja California, S of San Felipe, 25 November 1950.

ACKNOWLEDGMENTS

Collections in Mexico were under Mexican federal collecting permit (Permiso de Pesca de Fomento) DGOPA 14253. 101005.6950, and its extension DGOPA 06435.210606.2640,

issued to Findley and Jacobs by the Comisión Nacional de Acuacultura y Pesca of the Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA). Some California (USA) collections were made under California State Scientific Collecting Permit No. 2679 to Swift. Assistance with field sampling of specimens analyzed in this paper was provided by R. Hechinger, T. Baumiller, V. Cassano, D. Courtland, K. Lafferty, J. Lorda, J. Valencia, D. Wilde, and D. Yuan. Assistance with molecular and morphological analyses was provided by J. Lin, J. Krahelski, M. Kodomo, and G. Slater. Helpful advice, loan of material and specimens, and in some cases, laboratory work-space were generously provided by L. Parenti, J. Williams, and D. Pitassy (USNM), D. Buth (UCLA), C. Thacker, J. Seigel, and R. Feeney (LACM), H. Walker (SIO), P. Reinthal (UAZ), D. Nelson (UMMZ), P. Campbell (BMNH), T. Iwamoto, D. Catania, M. Hoang, J. McCosker, and J. Wong (CAS), and G. Bernardi (UCSC). We thank Mexico's Comisión Nacional de Acuacultura y Pesca of SAGARPA for granting the scientific collecting permits. Historical maps, used to determine type locality for *G. detrusus,* were provided by S. Nelson. R. Lea pointed us to another collection of *G. detrusus* in the CAS collections. P. Marsh provided advance drafts of the book, *Inland Fishes of the Greater Southwest*, for reference. Field and laboratory work was funded by UC MEXUS (to Jacobs and Findley), and by the University of California Genetic Resources Program.

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