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Redescription of the Texas Shiner *Notropis amabilis* from the southwestern United States and northern Mexico with the reinstatement of *N. megalops* (Teleostei: Cyprinidae)

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Notropis amabilis is redescribed based on type and non-type material from the United States (Texas and New Mexico) and Mexico. *Notropis megalops* is removed from the synonymy of *N. amabilis*, based on morphological and genetic evidence that the two represent distinct species, and redescribed based on type and non-type material from the United States (Texas) and Mexico. *Notropis amabilis* is distinguished from *N. megalops* based on differences in head and body pigmentation, body shape, and the shape of the metapterygoid in the hyopalatine arch. Molecular phylogenetic analyses of one mitochondrial gene (cyt *b*) and two nuclear genes (RAG1 and S7) and a concatenated data set consisting of all three genes for a small number of North American leuciscine cyprinids, including multiple members of the subgenus *Notropis*, places *N. amabilis* and *N. megalops* in different clades and never within a sister group relationship. The synonymy of *N. amabilis* and *N. megalops* is revised and lectotype designations are provided for *Alburnus amabilis*, *A. megalops* and *Cyprinella macrostoma*. A neotype is designated for *Cyprinella luxiliodes*, which is considered a junior synonym of *Cyprinella lutrensis*.

Introduction

Charles Frederic Girard described numerous new species of fishes, amphibians and reptiles from the southwestern and central United States, the majority of which were collected during the United States and Mexican 'boundary survey' (1851–1855) and Pacific railroad surveys (1853–1855). Arguably, one of Girard's most important contributions to our understanding of the ichthyofauna of this region is his monograph on the cyprinoid fishes found west of the Mississippi River Valley (Girard, 1856), which includes descriptions for approximately 190 species of the Cyprinidae and Catostomidae, over half of which were described for the first time. Despite the magnitude of his contributions, Girard is generally considered to have been a 'minor player' in the documentation of the North American fish fauna and even 'careless' by some of his contemporaries and successors who criticized him for publishing inadequate descriptions and apparently unnecessarily introducing multiple synonyms into the literature by describing the same species on

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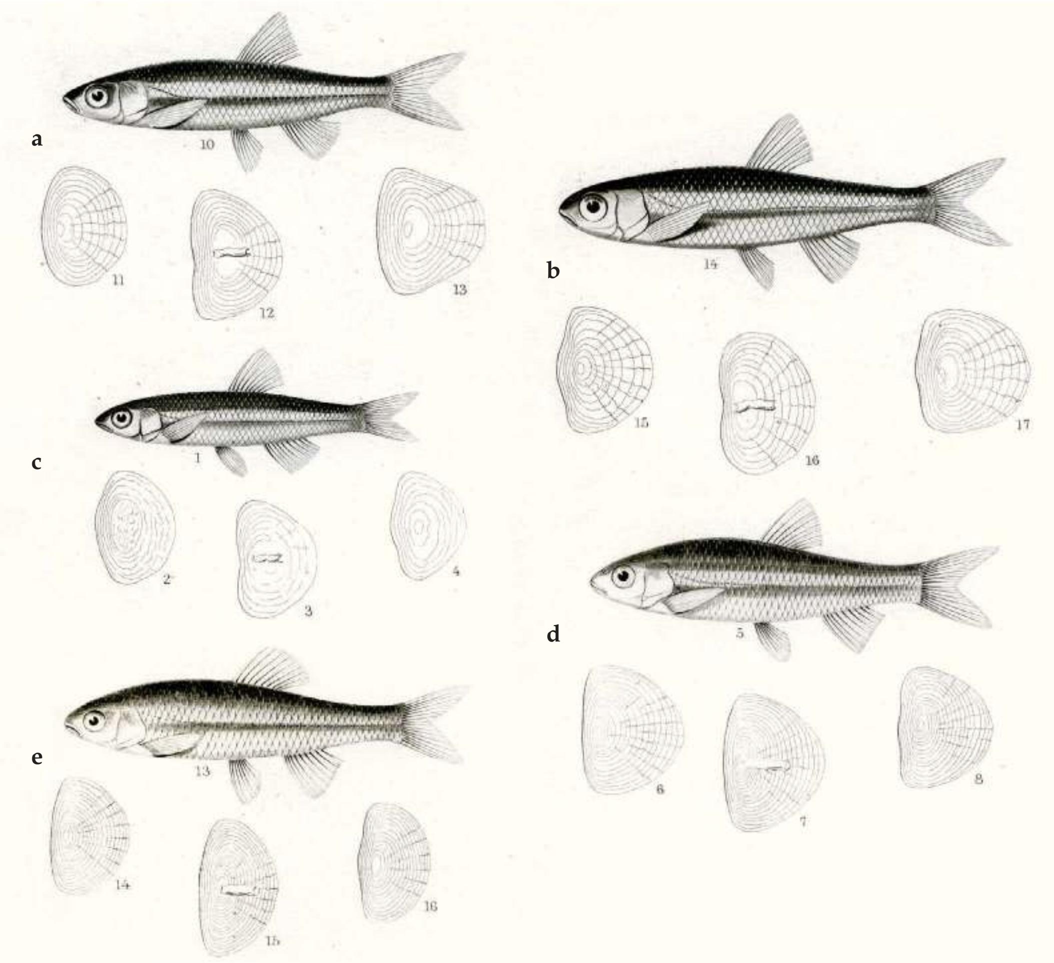

Fig. 1. Original illustrations of *Alburnus amabilis* and other taxa described by Girard (1856) that have been placed or tentatively placed in its synonymy. **a,** *A. amabilis*; **b,** *A. socius*; **c,** *A. megalops*; **d,** *Cyprinella macrostoma*; and **e,** *C. luxiloides*. Reproduced from Girard (1859: plates 29 and 31).

more than one occasion (reviewed by Jackson & Kimler, 1999). For example, five cyprinid species described by Girard (1856) from south central Texas and northern Mexico (viz. *Alburnus amabilis*, *A. megalops*, *A. socius*, *Cyprinella macrostoma* and *C. luxiloides*; Fig. 1) are considered to represent the same taxon, known currently as *Notropis amabilis* (Gilbert, 1978, 1998).

Notropis amabilis is a small species of shiner (maximum size 62 mm SL), common in small spring-fed creeks and rivers throughout the Gulf Coast drainages of central Texas (Brazos, Colorado, Guadalupe, San Antonio and Nueces) and the lower Rio Grande drainage of the United States and Mexico (Lee et al., 1980; Miller, 2005; Thomas et al., 2007; Hubbs et al., 2008; Page & Burr, 2011). Commonly referred to as the Texas shiner (Page et al., 2013), *N. amabilis* is a member of the subgenus *Notropis*; a grouping originally diagnosed by Coburn (1982) based on morphological characters to include (in addition to *N. amabilis*) *N. amoenus*, *N. ariommus*, *N. atherinoides*, *N. candidus*, *N. jemezanus*, *N. oxyrhynchus*, *N. perpallidus*, *N. photogenis*, *N. rubellus*, *N. scepticus*, *N. semperasper*, *N. shumardi*, *N. stilbius* and *N. telescopus*. Based on evidence from the cyt *b* gene, Bielawski & Gold (2001) removed *N. candidus* and *N. shumardi* from the subgenus

Fig. 2. *Notropis amabilis.* **a,** USNM 72, lectotype of *Alburnus amabilis*, 50.3 mm SL; USA: Texas: Leona River; **b,** MCZ 1798, lectotype of *Cyprinella macrostoma*, 45.5 mm SL; Mexico: China: Rio San Juan.

Notropis, and recognized the remaining 14 species as a monophyletic grouping with the addition of *N. suttkusi* and *N. girardi*. Within Bielawski & Gold's (2001) broader definition of the subgenus *Notropis*, *N. amabilis* was obtained as the sister taxon to *N. jemezanus*, a grouping also obtained by Schönhuth & Doadrio (2003) but not by Houston et al. (2010) based on analyses of the same mitochondrial gene. Recent phylogenetic investigations of North American minnows based on evidence from multiple mitochondrial and nuclear genes (e. g., Martin & Bonett, 2015) do not support monophyly of the subgenus *Notropis* as defined by Bielawski & Gold (2001) but obtain a monophyletic group comprising a subset of these taxa, including *N. amabilis*, *N. amoenus*, *N. ariommus*, *N. atherinoides*, *N. jemezanus*, *N. oxyrhynchus*, *N. rubellus*, *N. stilbius*, *N. suttkusi* and *N. telescopus* together with *N. micropteryx* and *N. percobromus*. The placement of *N. amabilis* within this latter group is largely unresolved (and without support values) (Martin & Bonett, 2015).

As part of our ongoing investigations of the phylogeographic and phylogenetic relationships of select species of North American minnows, we discovered unexpectedly high levels of genetic diversity between individuals of *N. amabilis* collected from adjacent drainages (Rio Grande and Nueces) within the state of Texas (southern United States). Further investigation of this and other material identified as *N. amabilis* revealed a number of morphological differences that were consistent with genetic differences. This suggested to us that *N. amabilis* (as currently defined; e. g., Miller, 2005; Hubbs et al., 2008; Page & Burr, 2011) may represent more than one species and prompted us to reconsider the synonymy of *N. amabilis* (Gilbert, 1978, 1998), populated entirely by names available from Girard (1856). In this paper we remove *A. megalops* from the synonymy of *N. amabilis*, recognize *N. megalops* as a valid species and provide redescriptions for both *N. amabilis* and *N. megalops,* based on type and non-type material.

Materials and methods

Morphological investigation. Specimens of *Notropis* utilized in this study were obtained from museum collections (abbreviations following Sabaj Perez, 2014). Measurements obtained from specimens generally follow those of Hubbs & Lagler (1958) and include: (1) standard length (SL), (2) head length (HL), (3) body depth (measured at origin of dorsal fin), (4) pre-dorsal length, (5) pre-pelvic length, (6) pre-anal length, (7) pre-anus length, (8) base of dorsal fin, (9) base of anal fin, (10 and 11) length of longest dorsal- and anal-fin ray (typically the last unbranched ray), (12) dorsal-caudal length, (13 and 14) length and depth of the caudal peduncle, (15 and 16) length of the upper and lower caudal-fin lobes, (17 and 18) head depth at orbit and occiput, (19) interorbital distance, (20) snout length, (21) snout to occiput, (22) orbit diameter, (23) width of mouth, and (24) length of lower jaw. Measurements are recorded as either a percentage of SL (2–16) or as a percentage of HL (17–24). External meristic characters used in this study generally follow those of Hubbs & Lagler (1958), except that we count lateral line bearing scales on the body and base of the caudal fin separately and recognize the last two fin rays that share a single pterygiophore in either the dorsal fin or anal fin as separate elements. Internal meristic characters were obtained from cleared and double stained specimens (c&s), prepared following the protocol of Taylor & Van Dyke (1985). Vertebral counts include the four Weberian centra and the terminal compound centrum (Fink & Fink, 1981). The number in parentheses following a meristic value denotes the frequency of that value. Terminology of the cranial skeleton follows Harrington (1955). Cleared and stained specimens (or parts thereof) were examined and photographed using a Zeiss SteREO Discovery V20 stereomicroscope equipped with a Zeiss Axiocam MRc5 digital camera.

Multivariate statistics. We utilized the PopTools add in (Hood, 2010) for Microsoft Excel® to conduct principal component analyses (PCA) on a data set of measurements obtained from 79 specimens representing three species of the subgenus *Notropis*, including *N. amabilis* (N = 40, 35.2–52.0 mm SL), *N. jemezanus* (N = 10, 36.8–68.5 mm SL) and *N. megalops* (N = 29, 36.4–50.0 mm SL). This data set comprised 20 of the 24 measurements listed above (excluding 10–11, 15–16). To remove the effects of overall body size, we regressed each measurement against SL and conducted PCA only on the residuals obtained from 19 of the 20 original measurements. A MANOVA was conducted on the PC axes contributing to 95 % of the cumulative variance using the statistical program JMP (with size effects calculated manually in Microsoft Excel® from the JMP output) to assess whether a significant difference existed between the data returned from the PCA for each species.

Molecular laboratory work and analysis of sequence data. A total of 112 individuals of *Notropis* (originally identified in the field as *N. amabilis*) were collected from 9 sites within the state of Texas, including locations within the Colorado, Guadalupe, San Antonio, Nueces, and Rio Grande river drainages. Specimens were euthanized upon capture with an overdose of MS222, preserved in 95 % ethanol, and subsequently maintained at 4 °C. Genomic DNA was extracted from muscle and/or fin clips using a DNeasy Tissue Extraction Kit (Qiagen, Inc., Valencia, CA, USA) following the manufacturer's protocols. The nearly complete mitochondrial cytochrome *b* (cyt *b*) gene was amplified using polymerase chain reaction (PCR) and the primer pair LA-danio and HA-danio (Mayden et al., 2007). Two single-copy nuclear loci were also amplified, including the S7 ribosomal protein gene intron 1 (S7) and the recombination activating protein 1 (RAG1), using the primer pairs S7RPEX1F and S7RPEX2R (Chow and Hazama, 1998) and R1 2533F and R1 4078R (Lopez et al., 2004), respectively. All PCR reactions were performed in 25.0 µl, containing 12.5 µl of GoTaq Green Master Mix (Promega, Madison, WI, USA), 5.5 µl of nuclease-free water, 300 ng of template DNA, and 2.0 µM of each primer (forward and reverse). PCR conditions follow those listed in Kim & Conway (2014). Amplified PCR products were sequenced using the HighThroughput sequencing facilities at Beckman Coulter Genomics (MA, USA). Obtained sequences were checked for accuracy of base determination using FinchTV v.1.4.0 (Geospiza, Inc.; http://www.geospiza.com/Products/finchtv.shtml) and assembled manually. All heterozygous nuclear sequences encountered were excluded from the study. Sequences of the three target genes were also obtained (as outlined above) or from Genbank (see Appendix 1) for the following taxa: *Agosia chrysogaster*, *Pimephales vigilax*, *Notropis jemezanus*, *N. atherinoides*, *N. percobromus*, *N. stilbius* and *N. hudsonius*. Novel sequences generated as part of this study have been deposited on Genbank (see Appendix 1).

Cyt *b* and RAG1 sequences were each aligned by eye using the program TextWrangler vs. 2.3 (Barebones Software Inc) and viewed in MacClade vs. 4.05 (Maddison and Maddison, 2005) to check for spurious stop codons. S7 sequence alignment was performed with MAFFT v.6.903 (Katoh and Toh, 2010) and checked manually for accuracy.

The final aligned individual gene data sets were comprised of the following number of aligned positions and individuals: 1137 base pairs (bp) of cyt *b* from 121 individuals; 1497 bp of RAG1 for 56 individuals; and 827 bp of S7 for 66 individuals. The three genes were also combined to form a concatenated data set, which was trimmed to include only unique mitochondrial haplotypes or nuclear alleles (3461 bp for 31 individuals).

Phylogenetic analyses were performed on the individual gene data sets under Maximum parsimony (MP) and Maximum likelihood (ML) criteria. MP analyses were implemented in PAUP* v. 4.0b10 (Swofford, 2002) using heuristic searches with tree-bisection and reconnection (TBR) branch swapping, with starting trees obtained by random stepwise addition (# reps 100). The maximum number of trees saved during each run was allowed to automatically increase by 100 and the MULTREES option was in effect. All characters were equally weighted and unordered and resulting equally parsimonious cladograms were rooted using *Agosia chrysogaster* and summarized using the strict consensus method. Nodal support was estimated using non-parametic bootstrapping (Felsenstein, 1985) for 1000 pseudoreplicates, utilizing a random addition sequence and TBR branch swapping. ML analyses were implemented in Garli v.0.951 (Zwickl, 2006) under a GTR (6 rate) model (all parameters estimated) with bootstrap analysis (100 replicates) and searches for the best-scoring ML tree conducted simultaneously.

We also conducted a Bayesian analysis of the combined dataset, partitioned by gene, using MrBayes v.3.2.1 (Ronquist et al., 2012). The best-fit models of sequence evolution were obtained for each gene using MrModeltest v2. (Nylander, 2004), based on the Akaike Information Criterion (Posada and Buckley, 2004). Two independent runs of 10^7 generations with four chains were performed for each gene, sampling trees every 1000 generations. Tracer v.1.5 (Rambaut & Drummond, 2009) was used to check convergence and stationarity, to determine the number of generations discarded as burn-in, and to confirm that effective sample size (ESS) values were over 200. Tree samples were used to construct a 50 % majority-rule consensus tree after discarding burn-in. The resulting tree was visualized in FigTree v.1.3.1 (http://tree.bio.ed.ac.uk/software/figtree).

Notropis amabilis (Girard, 1856)
(Figs. 2–4)

Alburnus amabilis Girard, 1856: 193; lectotype (by present designation) USNM 72 (Fig. 2a)
Cyprinella macrostoma Girard, 1856: 198; lectotype (by present designation) MCZ 1798 (Fig. 2b)

Material examined. United States: Texas: **Colorado River drainage:** TCWC 925.03, 109, 33.5–48.8 mm SL; Llano Co.: Llano River at Scotts Crossing, 30°43'39"N 98°48'47"W; 24 April 1976. – TCWC 928.02, 175, 22.6–52.1 mm SL; Blanco Co.: Cypress Creek at FM 962 crossing, 30°22'60"N 98°15'00"W; 24 April 1976. – TCWC 1131.01, 11, 29.4–37.1 mm SL; Gillespie Co.: small tributary of Pedernales River south of Kerrville; 5 May 1940. – TCWC 7823.02, 92, 27.7–51.1 mm SL; Irion Co.: Spring Creek at FM 915 crossing, 31°13'06"N 100°49'32"W; 14 May 1991. – TCWC 7824.03, 5, 35.8–42.0 mm SL; Tom Green Co.: Spring Creek at FR 2335 crossing, 31°19'48"N 100°38'22"W; 15 May 1991. – TCWC 7825.01, 37, 35.0–48.3 mm SL; TCWC 7825.07, 3 (c&s), 45.6–48.9 mm SL; Tom Green Co.: South Concho River, 1 mile north west of Christoval, 31°12'47"N 100°30'02"W; 17 May 1991. – TCWC 7826.02, 18, 31.1–47.8 mm SL; Tom Green Co.: Dove Creek at FR 2335, 31°16'25"N 100°37'49"W; 21 May 1991. – TCWC 7860.03, 262, 24.5–50.3 mm SL; Tom Green Co.: South Concho River at Head-of-the-River Ranch, 31°08'13"N, 100°29'40"W; 05 October 1991. – TCWC 1132.01, 26, 28.6–50.6 mm SL; San Saba Co.: Cherokee Creek 1.5 miles West of Cherokee, 30°58'21"N 98°46'45"W; 5 October 1940. – TCWC 1145.01, 24, 29.6–46.6 mm SL; Irion Co.: Spring Creek 0.5 miles south east of Mertzon, 31°15'09"N 100°48'53"W; 28 November 1964. – TCWC 1146.01, 18, 35.4–47.2 mm SL; Tom Green Co.: Dove Creek 1 mile North of Knickerbocker, 31°16'25"N, 100°37'49"W; 28 November 1964. – TCWC 11979.01, 989, 7.9–34.2 mm SL; Irion Co.: Spring Creek; 20 June 2001. – TCWC 11985.01, 36, 17.2–39.7 mm SL; Tom Green Co.: Dove Creek, pool below dam, 31°16'21"N 100°38'07"W; 21 June 2001. – TCWC 16322.10, 23 (DNA vouchers); TCWC 16322.11, 81, 32.7–44.1 mm SL; Kimble Co.: North Llano River at Rd 271, 30°30'56"N 99°48'20"W; 19 April 2013. – TCWC 16458.01, 10 (DNA vouchers); Tom Green Co.: South Concho River at Mineral Wells Rd crossing, 31°12'47"N 100°30'02"W; 9 August 2013. – TNHC 8195, 408, 25.1–43.4 mm SL; Tom Green Co.: South Concho River; 20 May 1958. **Guadalupe Drainage:** TCWC 234.01, 23, 36.3–51.2 mm SL; Comal Co.: Guadalupe River downstream from Canyon Dam at FM306 crossing, 29°51'40"N 98°09'31"W; 16 October 1971. – TCWC 962.03, 205, 21.0–39.9 mm SL; Kerr Co.: Guadalupe River at Kerrville; 20 July 1939. – TCWC 927.03, 36, 39.7–61.0 mm SL; TCWC 927.17, 5 (c&s), 39.0–49.7 mm SL; Hays Co.: San Marcos River at John J. Stokes Park, 29°52'18"N 97°55'54"W; 25 April 1976. – TCWC 1128.01, 32, 29.8–49.5 mm SL; Kerr Co.: Guadalupe River 1 mile upstream from Ingram,

Fig. 3. *Notropis amabilis*, TCWC 16878.05; USA: Texas: Nueces River. **a,** male, 42.0 mm SL; **b,** female, 39.4 mm SL.

Fig. 4. *Notropis amabilis*, photographed alive; **a,** TCWC 16879.08, male, 38.0 mm SL; USA: Texas: Frio River; **b,** TCWC 16878.05, male, 48.3 mm SL; USA: Texas: Nueces River.

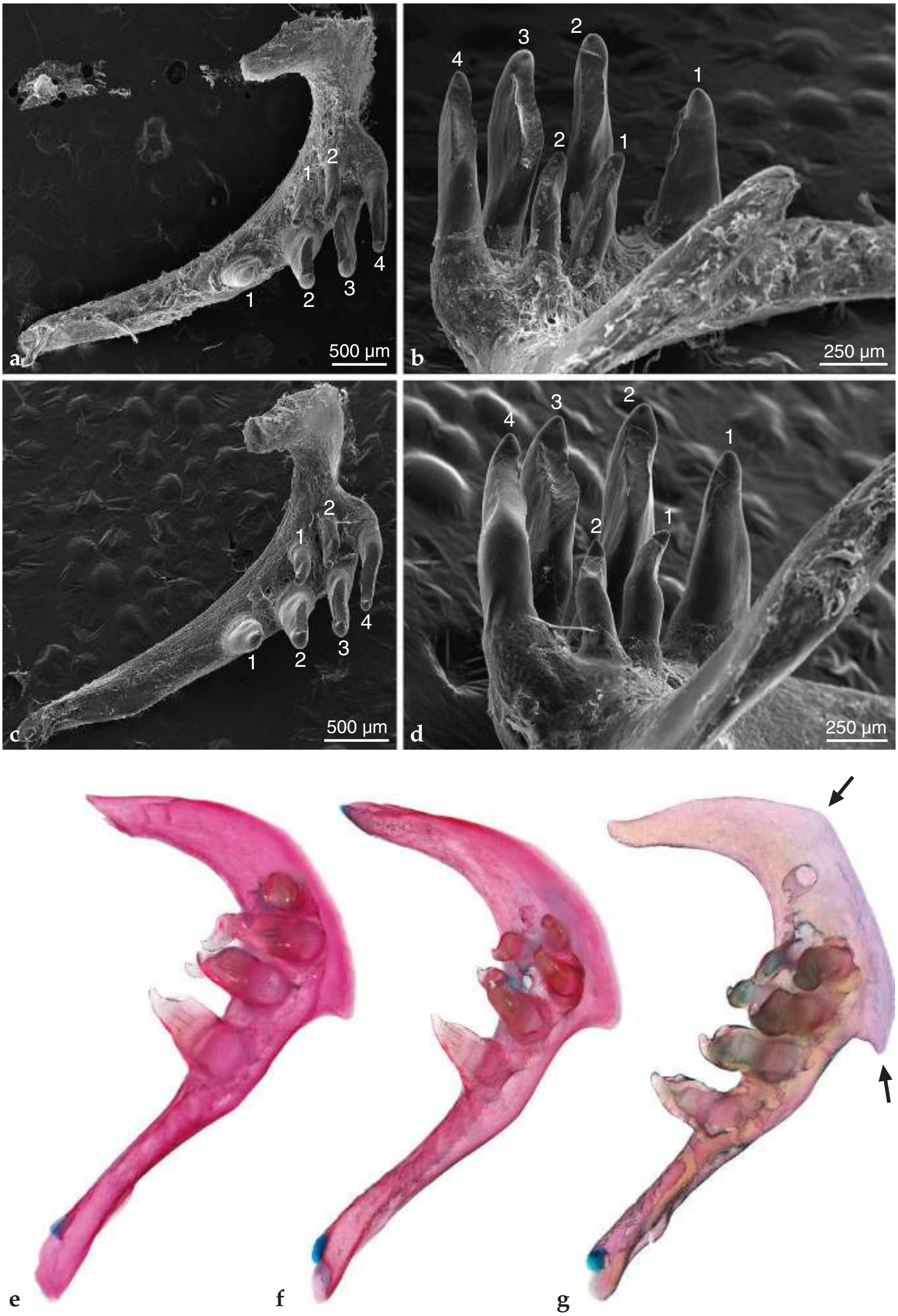

Fig. 5. Fifth ceratobranchial of: **a–b,** *Notropis amabilis*, USNM 427771, 45.0 mm SL; **c–d,** *N. megalops*, TCWC 3907.07, 39.0 mm SL; **e,** *N. amabilis*, TCWC 16457.09, 32.0 mm SL; **f,** *N. megalops*, TCWC 16457.08, 33.0 mm SL; **g,** *N. jemezanus*, TCWC 11045.01, 37.0 mm SL. Pharyngeal teeth are numbered 1–2 and 1–4 in the outer and inner rows, respectively in a–d. Arrows point to pronounced upper arch (upper arrow) and pronounced posteromedial hook (lower arrow) in ceratobranchial 5 in g.

30°04'13" N 99°15'21" W; 31 July 1939. – TCWC 1130.01, 4, 30.0–34.6 mm SL; Kerr Co.: North Fork of the Guadalupe River 4 miles upstream from Hunt, 30°03'36" N 99°23'45" W; 17 February 1940. – TCWC 1142.01, 4, 51.8–56.7 mm SL; Kerr Co.: North Fork of the Guadalupe River, 30°03'32" N 99°29'44" W; 6 January 1962. – TCWC 1144.01, 10, 37.9–42.2 mm SL; Comal Co.: Guadalupe River 12 miles north of New Braunfels, 29°51'51" N 98°09'50" W; 18 December 1960. – TCWC 3356.05, 212, 11.0–48.8 mm SL; Comal Co.: Honey Creek 9 miles northwest of Bulverde, 29°51'56" N 98°28'40" W; 3 December 1982. – TCWC 6221.01, 2, 49.5–50.0 mm SL; Kerr Co.: Guadalupe River at Mo-Ranch, 30°03'38" N 99°28'10" W; 20 April 1985. – TCWC 6224.01, 1, 42.2 mm SL; Comal Co.: Guadalupe River Spring Branch, 29°52'28" N 98°29'01" W; 3 May 1985. – TCWC 1422.03, 1, 35.5–36.5 mm SL; Hays Co.: San Marcos River in San Marcos, 29°52'42" N 97°55'58" W; 12 November 1960. – TCWC 1788.02, 1, 39.9 mm SL; Hays Co.: Blanco River 1 mile east of San Marcos, 29°52'47" N 97°54'37" W; 12 March 1977. – TCWC 2825.07, 124, 22.5–49.9 mm SL; Comal Co.: Guadalupe River at New Braunfels, 29°45'38" N 98°08'16" W; 20 April 1980. – TCWC 14685.06, 17, 45.0–53.0 mm SL; Hays Co.: San Marcos River at Cape Road crossing, 29°52'07" N 97°55'51" W; 21 April 2009. – TCWC 15547.05, 1, 37.0 mm SL; Kerr Co.: Guadalupe River at La Casita crossing, 30°00'30" N 99°24'27" W; 15 October 2011. – TCWC 15548.02, 1 (DNA voucher); Kerr Co.: Johnson Creek at Byas Spring Road crossing, 30°08'49" N 99°20'18" W; 15 October 2011. – TCWC 16404.08, 23, 24.0–44.2 mm SL; TCWC 16404.12, 4 (DNA vouchers); Hays Co.: Blanco River at Hidden Valley Road crossing, 29°59'08" N 98°03'54" W; 11 October 2012. – TNHC 16919, 39, 18.0–58.5 mm SL; Kerr Co.: South Fork Guadalupe River at Lynx Haven Springs, 29°58'59" N 99°27'31" W; 12 June 1986. **San Antonio Drainage:** TCWC 169.02, 18.6–47.9 mm SL; Bandera Co.: Medina River at Medina, 29°47'38" N 99°14'55" W; 27 November 1950. – TCWC 1140.01, 41.6 mm SL; Bexar Co.: Salado Creek 5 miles south of San Antonio, 29°16'30" N 98°25'56" W; 23 September 1960. – TCWC 16329.07, 33 (DNA vouchers); TCWC 16329.08, 148, 21.0–50.5 mm SL; Bandera Co.: North Prong of Medina River at Robertson Creek Road, 29°48'58" N 99°15'33" W; 21 April 2013. **Nueces River Drainage:** TCWC 6225.01, 1, 46.8 mm SL; Edwards Co.: Nueces River at Hwy 335 crossing north of Barksdale, 29°48'18" N 100°01'07" W; 2 May 1985. – TCWC 6668.04, 100, 14.2–49.5 mm SL; TCWC 6668.12, 5 (c&s), 39.5–43.0 mm SL; Zavala Co.: Nueces River at Pryor Ranch,

Table 1. Morphometric data for *Notropis amabilis* (n = 47) and *N. megalops* (n = 33).

	N. amabilis			*N. megalops*		
	range	mean	SD	range	mean	SD
Standard length (mm)	35.2–52.0			36.4–50.0		
In percent of standard length						
Head length	22.5–27.6	25.3	1.2	24.6–29.4	27.0	1.2
Body depth	17.7–24.0	21.1	1.4	19.0–24.2	21.6	1.4
Pre-dorsal length	49.4–55.2	53.0	1.3	50.3–54.7	52.6	1.1
Pre-pelvic length	46.4–52.1	49.8	1.3	46.8–52.7	49.3	1.4
Pre-anal length	62.0–69.7	65.9	1.7	61.9–69.3	65.2	1.7
Pre-anus length	59.2–65.6	62.3	1.7	59.3–67.4	63.4	1.8
Base of dorsal fin	9.8–13.4	11.5	0.9	9.5–12.7	10.8	0.7
Length of longest dorsal-fin ray	17.5–23.6	20.1	1.5	17.6–22.2	19.8	1.1
Base of anal fin	11.5–15.4	13.1	0.9	10.9–14.5	12.6	0.9
Length of longest anal-fin ray	12.9–16.9	15.1	1.0	12.9–17.0	15.0	1.2
Dorsal-caudal length	46.8–54.8	50.4	1.7	46.4–54.8	49.5	1.5
Length of caudal peduncle	18.8–26.0	21.8	1.4	20.3–24.6	22.4	1.0
Depth of caudal peduncle	8.4–10.6	9.7	0.5	8.5–10.6	9.6	0.6
Length of upper caudal-fin lobe	20.4–27.6	23.5	1.6	21.9–26.5	24.1	1.4
Length of lower caudal-fin lobe	22.7–28.9	25.2	1.4	21.3–27.5	24.6	1.6
In percent of head length						
Head depth at orbit	47–58	52.6	2.6	50–58	53.4	2.5
Head depth at occiput	57–69	62.6	2.9	60–73	64.6	3.3
Interorbital distance	29–40	34.4	2.4	26–37	31.0	2.3
Snout length	20–30	25.5	2.4	21–36	26.3	2.6
Snout to occiput	69–87	78.8	3.7	70–84	78.8	3.3
Orbit diameter	29–36	32.1	1.6	28–36	32.0	1.9
Width of mouth	17–25	20.4	1.6	17–26	21.3	2.3
Length of lower jaw	27–36	32.2	2.2	30–40	34.5	2.2

28°47'58" N 99°49'17" W; 22 May 1986. – TCWC 11993.01, 40, 19.6–27.4 mm SL; Real Co.: West Frio River on Old Rock Springs Road, 29°51'47" N 99°46'20" W; 29 June 2001. – TCWC 12013.01, 1, 28.6 mm SL; Uvalde Co.: Sabinal River at Hwy 1050 crossing, 29°36'43" N 99°31' 48" W; 11 July 2001. – TCWC 12020.01, 83, 17.6–45.7 mm SL; Bandera Co.: Mill Creek at Ranch Dos Arroyos off Hwy 342, 29°45'05" N, 99°31'55" W; 12 July 2001. – TCWC 16326.12, 13 (DNA vouchers); TCWC 16326.13, 60, 23.2–52.0 mm SL; Uvalde Co.: Nueces River at FM 55, 29°37'04" N 100°00'33" W; 20 April 2013. – TCWC 16327.17, 12 (DNA vouchers); TCWC 16327.18, 28, 24.6 –43.5 mm SL; Uvalde Co.: Frio River at FM 1050, 29°36'18" N 99°44'17" W; 21 April 2013. – TNHC 45623, 177, 21.4–53.7 mm SL; Nueces River; 24 April 2008. – TNHC 45631, 35, 22.9–47.4 mm SL; Frio River; 11 June 2007. – TNHC 45651, 173, 30.9–51.4 mm SL; Nueces River; 12 June 2007. – USNM 72, lectotype of *Alburnus amabilis*, 50.3 mm SL; USNM 427771, 25 paralectotypes of *Alburnus amabilis*, 43.0–49.0 mm SL; Uvalde Co.: Leona River, near Uvalde; 1851. **Rio Grande Drainage:** United States: New Mexico: UMMZ 66127, 9, 31.8–44.0 mm SL; Chaves Co.: Middle Brendo Creek near Roswell, 33°26'17" N 104°29'48" W; 2 April 1916. – UMMZ 66152, 4, 48.5–49.4 mm SL; Chaves Co.: South Spring River, south of Roswell, 33°24'18" N 104°31'11" W; 3 April 1916. Texas: OMNH 85479, 1, 46.8 mm SL; Val Verde Co.: Devils River at Bakers Crossing, FM 163, 29°58'02" N 101°08'57" W; 27 June 1995. – TCWC 15558.12, 4, 34.3–37.6 mm SL; TCWC 15558.12, 1 (c&s), 39.0 mm SL; same locality; 20 November 2011. – TCWC 16325.12, 14 (DNA vouchers); TCWC 16325.13, 24, 18.1–34.0 mm SL; same locality; 20 April 2013. – TCWC 16457.01, 5 (DNA vouchers); TCWC 16457.09, 1 (c&s), 32.0 mm SL; same locality; 3 August 2013. – TCWC 7512.04, 1, 42.1 mm SL; Val Verde Co.: Devils River upstream of Dolans Falls, 29°53'26" N 100°59'37" W; 19 November 1993. – TNHC 29486, 38, 20.0–52.1 mm SL; Val Verde Co.: Devils River; 31 July 2001. – TNHC 21964, 5, 23.5–29.6 mm SL; Kinney Co.: Pinto Creek at HW 90, 29°20'07" N 100°32'01" W; June 1990. – TNHC 29466, 310, 13.0–45.4 mm SL; Kinney Co.: Pinto Creek, 29°24'40" N 100°27'06" W; 6 April 2002. – TNHC 1851, 2, 35.6–37.7 mm SL; Kinney Co.: Los Mores Creek at Brackettville, 29°18'28" N 100°25'08" W; 14 April 1951. – TNHC 22221, 1, 34.1 mm SL; Kinney Co.: Sycamore Creek, 29°15'15" N 100°45'03" W; 12 June 1990. – TNHC 24680, 5, 37.1–40.9 mm SL; Maverick Co.: Rio Grande 14 KM downstream from Eagle Pass, 28°37'13" N 100°26'51" W; 22 March 1993. Mexico: Nuevo Leon: MCZ 1798, lectotype of *Cyprinella macrostoma*, 45.5 mm SL; Rio San Juan in the vicinity of China; 1853. – TNHC 1661, 35, 30.3–39.1 mm SL; Rio Sabinas de Nuevo Leon, 2 miles south west of Sabinas Hidalgo, 26°29'14" N 100°13'24" W; 8 June 1951. – TNHC 5843, 10, 25.0–32.8 mm SL; Rio Salado 8 miles south west of Anuhuac, 27°11'12" N 100°10'03" W; 12 June 1951. – UMMZ 97434, 35, 31.0–41.0 mm SL; Rio San Juan at San Juan, East of Monterrey, 25°32'32" N 99°50'08" W; 16 April 1930. – UMMZ 169590, 28, 28.5–39.4 mm SL; Rio San Juan in the vicinity of China, 25°45' N 99°15' W; 16 December 1941. Coahuila: KU 41373, 15, 39.1–49.3 mm SL; overflow of Presa Don Martin, 27°30'59" N 100°36'37" W; 12 March 1934. TNHC 1721, 1, 36.7 mm SL; Rio Sabinas de Coahuila 5 miles north west of Villa Juarez, 27°38'33" N 100°47'49" W; 15 June 1951. – TNHC 1727, 36, 21.7–39.5 mm SL; Rio Sabinas de Coahuila 2 miles north of Musquiz, 27°58'09" N 101°34'50" W; 16 June 1951. – TNHC 5942, 1, 32.9 mm SL; Rio Sabinas de Coahuila 2 miles south west of Nueva Rosita, 27°55'24" N 101°14'19" W; 15 June 1951.

Table 2. Meristic characters of *Notropis amabilis* and *N. megalops*. Values reported for fin and vertebrae characters are derived from c&s specimens of *N. amabilis* (n = 15) and *N. megalops* (n = 7). Values for scale characters are derived from alcohol specimens of *N. amabilis* (n = 47) and *N. megalops* (n = 33).

	N. amabilis		*N. megalops*	
	range	mode	range	mode
Dorsal-fin rays	10–11 (iii.7–8)	iii.8	11 (iii.8)	–
Anal-fin rays	11–14 (iii.8–11)	iii.9	13–14 (iii.10–11)	iii.10
Pectoral-fin rays	13–16 (i.12–16)	i.14	14–15 (i.13–14)	i.13
Pelvic-fin rays	8 (i.7)	–	8 (i.7)	–
Caudal-fin rays	10+9	–	10+9	–
Dorsal procurrent rays	9–11	11	8–12	9
Ventral procurrent rays	7–9	8	8–11	8
Total vertebrae	36–38	37	37–38	37
Abdominal vertebrae	17–19	19	18–20	18
Caudal vertebrae	17–19	18	18–19	19
Scales in lateral line scale row	35–37	36	35–38	36
Predorsal scales	14–20	16	14–17	14
Circumferential scales	14–18	18	16–20	18
Circumpeduncular scales	12–14	12	12–16	14

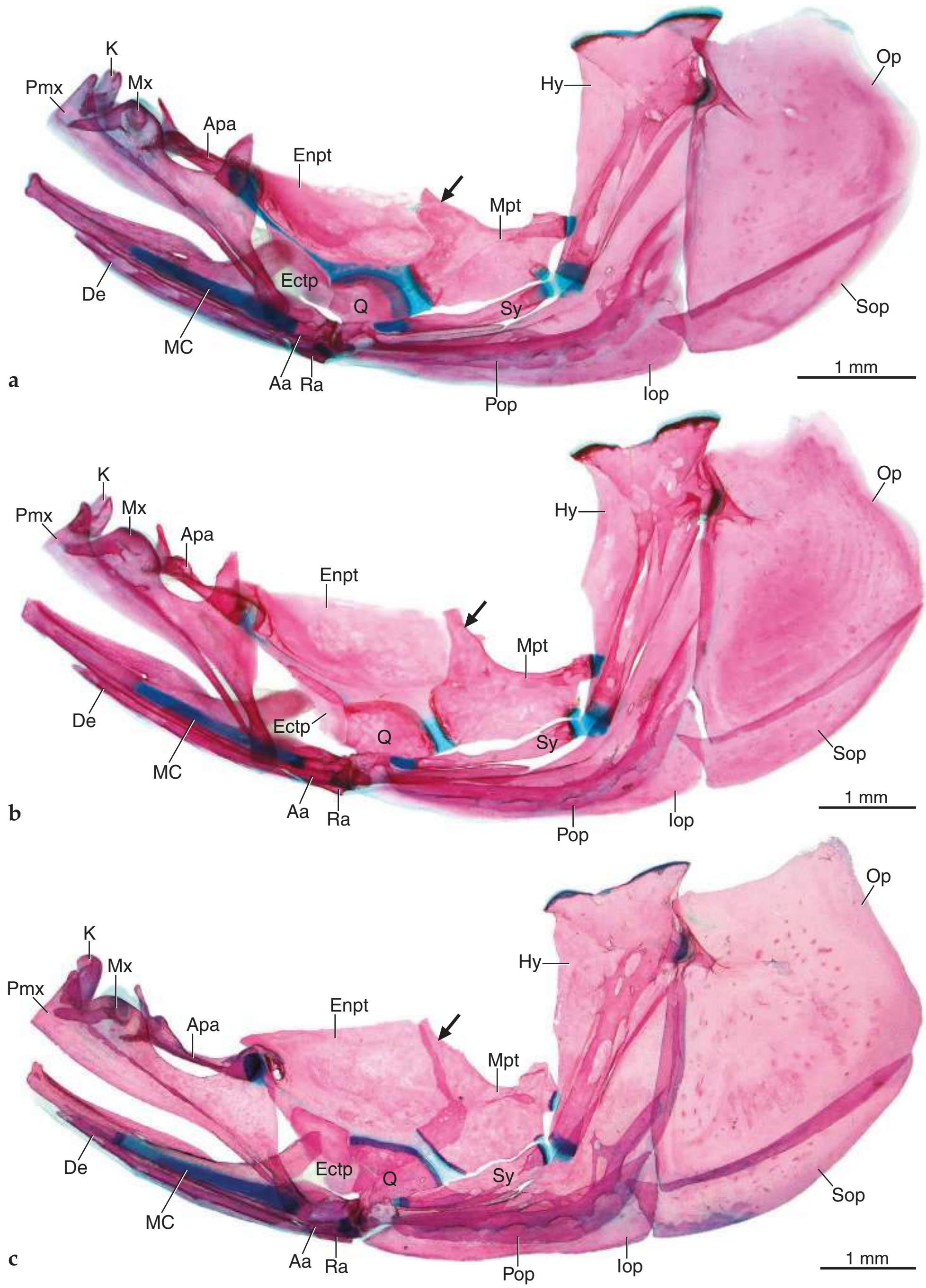

Fig. 6. Hyopalatine arch of right side in lateral view of: **a,** *Notropis amabilis*, TCWC 16457.09, 32.0 mm SL; **b,** *Notropis megalops*, TCWC 16457.08, 33.0 mm SL; **c,** *N. jemezanus*, TCWC 11045.01, 37.0 mm SL. Arrow points to anterodorsal process of metapteryoid. Abbreviations: **Aa**, anguloarticular; **Apa**, autopalatine; **De**, dentary; **Ecpt**, ectopterygoid; **Enpt**, endopterygoid; **Hy**, hyomandibular; **Iop**, interopercle; **K**, kinethmoid; **MC**, Meckel's cartilage; **Mpt**, metapterygoid; **Mx**, maxilla; **Op**, opercle; **Pmx**, premaxilla; **Pop**, preopercle; **Q**, quadrate; **Ra**, retroarticular; **Sop**, subopercle; **Sy**, symplectic.

Fig. 7. Close up of head (in dorsal, lateral and ventral view) in males of: **a,** *Notropis amabilis*, TNHC 29486, 38.8 mm SL; and **b,** *N. megalops*, THNC 58718, 36.8 mm SL.

Diagnosis. *Notropis amabilis* is a member of subgenus *Notropis* (sensu Bielawski & Gold, 2001). It is distinguished from all other members of the subgenus except *N. megalops* by the following combination of characters: lateral line scales most commonly 36 (range 35–37); circumpeduncle scale rows most commonly 12 (range 12–14); predorsal scales most commonly 16 (range 14–20); gill rakers on first gill arch 8–9; anal-fin rays most commonly iii.9 (range iii.8–iii.11); total number of pelvic-fin rays 8 (i.7); total number of vertebrae most commonly 37 (range 36–38); upper arm of ceratobranchial 5 weakly arched; lower lip with dark brown pigmentation; dark lateral stripe well developed. *Notropis amabilis* is distinguished from *N. megalops* by the following combination of characters: body depth greatest at point approximately midway between insertion of pectoral and pelvic fins (vs. greatest at point slightly posterior to insertion of pectoral fin); anterodorsal process of metapterygoid broad and triangular (vs. slender and pointed); dorsal surface of head and snout uniformly light brown in life (vs. dorsal surface of snout and interorbital region of head with black to dark brown pigment arranged as a narrow stripe anteriorly along dorsal midline of snout); dark brown stripe along dorsal midline anterior to dorsal-fin origin weakly developed and of uniform width (vs. dark brown stripe along dorsal midline anterior to dorsal-fin origin well developed, widest posteriorly directly anterior to dorsal-fin origin); and anterior portion of lateral line (anterior to vertical through anal-fin origin) bordering ventral margin of dark lateral stripe (vs. disjunct from ventral margin of dark lateral stripe).

Description. General body shape as in Figures 2–4. Morphometric characters are listed in Table 1 and meristic characters in Table 2. Small cyprinid fish, maximum size recorded 58.5 mm SL. Body slightly laterally compressed, fusiform. Dorsal profile weakly arched, rising gradually from snout to dorsal-fin origin, sloping gently towards caudal-fin base. Ventral profile convex anterior to anal-fin origin, weakly concave from anal-fin origin to caudal-fin base. Body depth greatest at point approximately midway between insertion of pectoral and pelvic fins; narrowest at midpoint of caudal peduncle. Head and eye relatively large. Pupil elliptical, pointed anteriorly. Mouth large, terminal, posteriormost tip of upper jaw situated below anterior margin of orbit, not reaching to vertical through anterior margin of pupil. Lips thin, smooth, of uniform thickness along length of upper jaw; lower lip not obscured by upper lip in dorsal view. Snout moderately pointed, tip located along horizontal through center of pupil. Nostrils located closer to anterior margin of eye than tip of snout. Anterior nostril small, crescent shaped; separated from larger posterior nostril by low flap of skin. Skin surrounding nostrils and along anterodorsal margin of orbit depressed, creating a distinct groove along dorsolateral surface of head, from nostril to horizontal through center of orbit. Gill membranes joined to isthmus anteriorly.

Typically four infraorbital bones (IO1–4). IO1 a flat, elongate rectangular bone, with pronounced projection along dorsal margin. IO2–4 narrow tube-like bones, composed predominantly of sensory canal ossification. IO2 or IO3 divided into two smaller ossifications in few individuals. Cephalic lateral line system well developed; composed of following sensory canals and externally visible pores: infraorbital sensory canal with 11 (3) or 12 (1) pores; supraorbital sensory canal with 7 (3) or 8 (1) pores; preopercular-mandibular sensory canal with 11 (3) or 12 (1) pores (including 4 (3) or 5 (1) in mandibular portion and 7 in preopercular portion); otic sensory canal with 5 pores; and temporal sensory canal with 3 pores. Number of pores in cephalic sensory canals typically asymmetrical. Supraorbital sensory canal with well-developed parietal branch; disjunct from infraorbital and otic sensory canals. Preopercular-mandibular sensory canal terminating along posterior edge of preopercle about midway along vertical arm of bone; disjunct from otic sensory canal.

Pharyngeal teeth 2,4–4,2; slender, unicuspid, with weak dorsally directed distal hook (Fig. 5a–b). Upper arm of ceratobranchial 5 weakly arched (Fig. 5e). Anterior edge of first gill arch with 8–9 small, slender, dagger-like gill raker ossifications; 6–7 along lower limb, 2 along upper limb. Gill rakers along posterior edge of first gill arch, anterior and posterior edges of second to fourth, and anterior edge of fifth tiny, triangular-shaped bones. Metapterygoid with broad anterodorsal process bordering posterodorsal edge of endopterygoid (Fig. 6a). Basioccipital process with well developed masticatory plate and pharyngeal process; pharyngeal process rounded posteriorly; terminating directly below 4th vertebral centrum. Hyoid bar with three falciform branchiostegal rays. Basihyal long and slender.

Dorsal-fin rays iii.7 (1) or iii.8 (14). Anal-fin rays iii.8 (1), iii.9 (9), iii.10 (3) or iii.11 (1). Principal caudal-fin rays 10 + 9; dorsal procurrent rays 9 (5), 10 (5) or 11 (5); ventral procurrent rays 7 (1), 8 (9) or 9 (5). Pectoral-fin rays i.12 (4), i.13 (3), i.14 (5), i.15 (2); pelvic fin rays i.7. Dorsal fin high, triangular with weakly rounded tip; posterior margin weakly concave. Anal fin roughly triangular in shape; posterior margin concave. Anal-fin base longer than dorsal-fin base. Origin of anal fin posterior to vertical line through insertion of last dorsal-fin ray. Caudal fin forked; tip of upper and lower lobe rounded; upper and lower lobes equal in length or lower lobe slightly longer than upper lobe. Pectoral fin large, triangular; posterior margin rounded. Pelvic fin small, approximately half of pectoral fin, triangular; posterior margin rounded. Insertion of pelvic fin anterior to vertical line through dorsal-fin origin.

Scales cycloid, large, with few well-developed radii over posterior field of scale body. Lateral line complete, with 35 (13), 36 (23) or 37 (9) scales, plus 1 (24) or 2 (20) on base of caudal fin. Scales in predorsal scale row 14 (4), 15 (8), 16 (17), 17 (8), 18 (5), 19 (2) or 20 (1). Circumferential scale rows 16 (17) or 18 (25), including 5 (15) or 6 (28) above lateral line and 2 (3) or 3 (39) below lateral line. Circumpeduncular scale rows 12 (43) or 14 (2). Ventral surface between pectoral fins with complete covering of scales. Total number of vertebrae 36 (3), 37 (11) or 38 (1), consisting of 17 + 19 (1),

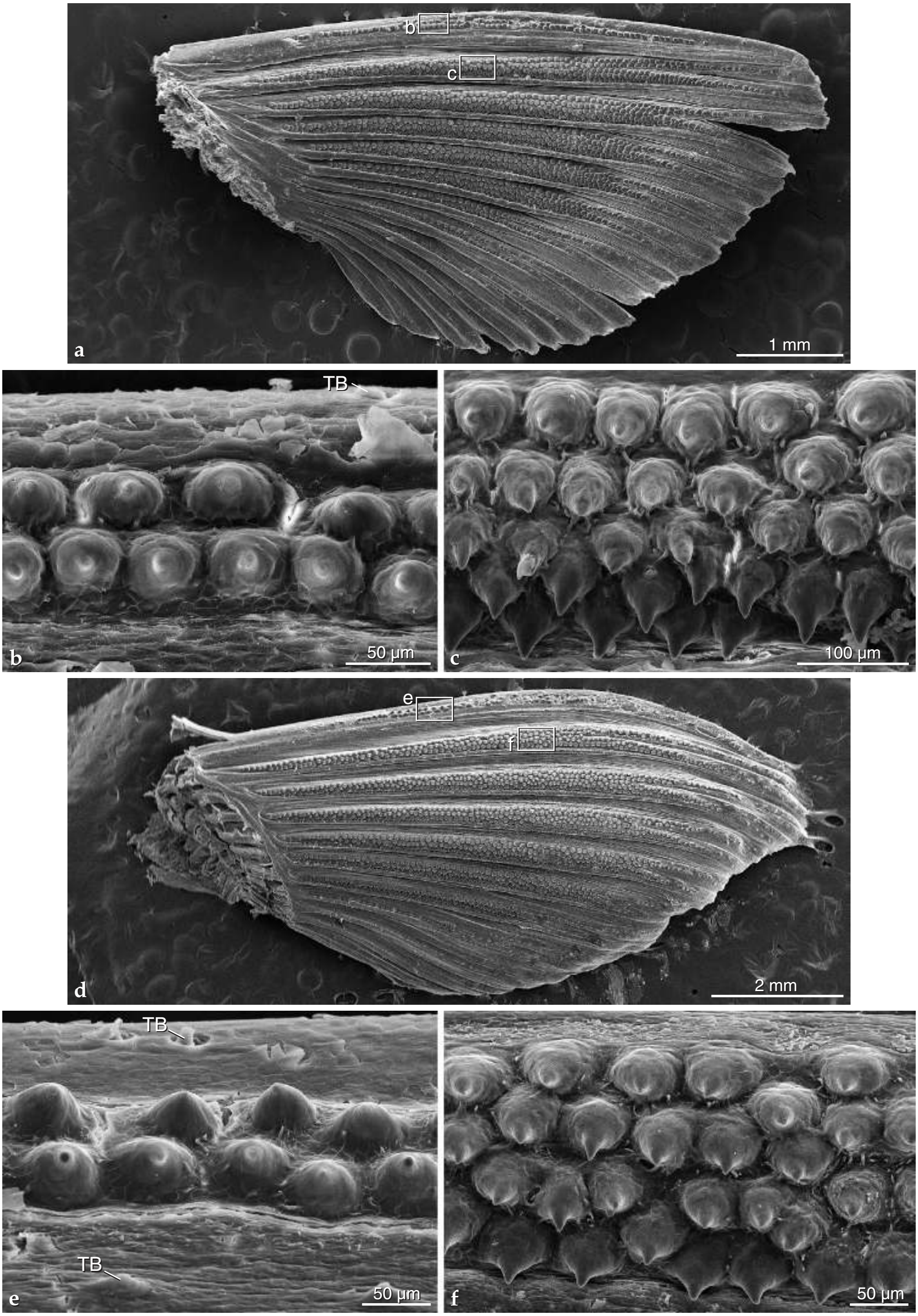

Fig. 8. Scanning electron micrographs of pectoral fin tuberculation in males of: **a–c,** *Notropis amabilis*, TCWC 16322.11, 38.0 mm SL; and **d–f,** *N. megalops*, TCWC 7518.04, 42.0 mm SL. Boxes in a and d represent approximate position of tubercles shown in b/c and e/f, respectively. **TB**, taste bud.

Fig. 9. Pigmentation along predorsal midline in: **a–c,** *Notropis amabilis*, THNC 29486 (a, 25.6 mm SL; b, 31.1 mm SL; c, 38.8 mm SL); and **d–f,** *N. megalops*, TNHC 58718 (d, 22.2 mm SL; e, 27.2 mm SL; f, 36.8 mm SL).

18 + 18 (1), 19 + 17 (1), 19 + 18 (11) or 19 + 19 (1) abdominal and caudal vertebrae.

Small conical tubercles, with pointed tip, irregularly scattered over entire dorsal surface of head, lateral surface of head along dorsal margin of preopercular portion of preopercular sensory canal, and lower jaw in males (Fig. 7a). Scales along dorsal midline between occiput and dorsal-fin origin with irregular scattering of minute conical tubercles in males. Scales on dorsolateral body surface directly posterior to head edged with 4–6 minute conical tubercles in males. Dorsal surface of 8–9 anteriormost pectoral-fin rays with minute conical tubercles, with slightly recurved tip, arranged in regular rows in males. Tubercles on dorsal surface of anteriormost pectoral-fin ray arranged predominantly in a single row, with shorter second row present midway along length of ray (Fig. 8a–b). Tubercles on dorsal surface of second-eight/ninth pectoral-fin rays arranged in multiple rows (Fig. 8c), with number of rows decreasing posteriorly. Females with minute conical tubercles irregularly scattered over dorsal surface of head and lower jaw only.

Coloration. In alcohol, body background colour light cream (Fig. 3). Occiput and interorbital region dark brown. Dorsal surface of snout weakly speckled with dark brown melanophores (Fig. 7a). Faint dark brown stripe along dorsal midline from occiput to caudal fin base, interrupted along base of dorsal fin (Fig. 9a). Narrow dark brown lateral stripe along body side from gill opening to base of caudal fin, continued on posterior half of head by dense scattering of dark brown melanophores over upper half of opercle. Anterior half of lateral stripe on body diffuse, comprised of scattered dark brown melanophores; posterior half of lateral stripe notably darker than anterior half, comprised of densely arranged dark brown melanophores.

Anterior half of lateral stripe flanked dorsally and ventrally by scattering of small dark brown melanophores in tuberculate males. Scales above lateral stripe edged posteriorly with dark brown melanophores. Scales below lateral line scale row without pigment. Few scattered dark brown melanophores around pore of lateral line canal along first five to ten scales in lateral line scale row, around base of anal-fin rays, around ventral margin of eye, lateral surface of snout and upper lip. Ventral surface devoid of pigment except for few scattered melanophores at symphysis of lower jaw. Few dark brown melanophores along branched dorsal-fin rays, densest around proximalmost fork in rays, forming indistinct stripe across center of fin. Caudal fin with small dark brown melanophores located along length of principal caudal-fin rays. Small dark brown melanophores along dorsal surface of anteriormost pectoral-fin ray in both sexes and dorsal surface of four to five anteriormost branched pectoral-fin rays in males. Pelvic and anal fins immaculate.

In life, body semi-translucent (Fig. 4a). Peritoneal lining white to silvery; visible through body musculature below lateral line anterior to anus. Dorsal surface of head and eyes with golden brown sheen. Lateral stripe indistinct, bordered dorsally by a thin green-golden stripe. Dark brown melanophores around posterior edge of scales dorsal to lateral stripe distinct, forming obvious reticulate pattern over dorsal surface of body. Dorsal midline with obvious green-golden stripe (Fig. 4b). Scales in third scale row along side of body with small patch of blue iridiophores at center, forming series of indistinct blue spots along upper side of body, most obvious along posterior half of body in dorsal view. Dark brown pigmentation on fins indistinct.

Distribution. *Notropis amabilis* is widely distributed throughout the upper portions of the Colorado, Guadalupe, San Antonio and Nueces drainages of Texas (United States) and sporadically throughout the Rio Grande drainage, in both the United States (Texas) and Mexico (Coahuila and Nuevo Leon) (Fig. 10). *Notropis amabilis* is also known from a small number of collections from tributaries of the Pecos River (Rio Grande Drainage) around Roswell, New Mexico (United States), but is considered to have been extirpated from New Mexico (Sublette et al., 1990). We have also examined material identified as *N. amabilis* from the Rio Conchos (Chihuahua, Mexico) comprising juvenile specimens (26–30 mm SL). Though this material corresponds well with *N. amabilis* in external appearance and meristic characters we are currently uncertain about identification and refer to this material as *N.* cf. *amabilis* for the time being.

Girard (1856: 198) reports that the syntypes of *Alburnus amabilis* were obtained from the Leona River (Nueces drainage). The Leona River runs through the city of Uvalde (Uvalde County, Texas) and has been significantly altered (impounded and channelized) since the 1850s. Despite multiple attempts, we have been unable to collect *N. amabilis* from the Leona River within the city limits of Uvalde or immediately downstream.

Notropis megalops (Girard, 1856)
(Figs. 11–13)

Alburnus megalops Girard, 1856: 193; lectotype (by present designation) MCZ 1682 (Fig. 11a)
Alburnus socius Girard, 1856: 193; lectotype (by present designation) USNM 39654 (Fig. 11b)
Notropis swaini Jordan & Gilbert, in Jordan, 1885: 123 (unnecessary replacement name for *Alburnus megalops* Girard, 1856)

Material examined. All Rio Grande Drainage. United States: Texas: MCZ 1682, lectotype of *A. megalops*, 39.7 mm SL; MCZ 171862, paralectotype of *A. megalops*, 36.5 mm SL; Val Verde Co.: San Felipe Creek. – TCWC 6241.01, 5, 30.9–40.7 mm SL; TCWC 6242.03, 47, 30.9–42.9 mm SL; TCWC 6243.05, 17, 25.0–42.0 mm SL; Val Verde Co.: San Felipe Creek at Moody Ranch, 1 mile south of Del Rio, 29°19'56"N 100°53'16"W; 27–28 May 1985. – TCWC 11044.01, 20, 26.2–46.9 mm SL; Val Verde Co.: San Felipe Creek at Lowe Ranch; 14 March 1979. – TCWC 11880.01, 48, 13.9–24.9 mm SL; Val Verde Co.: San Felipe Creek 30 meters upstream from confluence with east spring outflow, 29°22'18"N 100°53'02"W; 3 August 2001. – TCWC 11882.01, 69, 18.5–44.3 mm SL; same locality; 23 March 2002. – TCWC 11884.01, 52, 13.9–35.9 mm SL; Val Verde Co.: San Felipe Creek in Del Rio Golf Course, 29°22'14"N 100°53'04"W; 3 November 2001. – TCWC 11885.01, 35, 21.0–37.9 mm SL; same locality; 23 March 2002. – TCWC 13087.08, 2, 17.8–24.3 mm SL; same locality; 21 September 2002. – TNHC 9461, 43, 33.3–51.4 mm SL; same locality; 14 March 1979. – TCWC 11888.01, 21, 25.0–45.0 mm SL; TCWC 11888.11, 3 (c&s), 38.0–42.0 mm SL; Val Verde Co.: San Felipe Creek in Del Rio city park, 29°21'47"N 100°53'17"W; 3 August 2001. – TCWC 11889.01, 4, 34.4–40.9 mm SL; same locality; 3 November 2001. – TCWC 11890.01, 2, 36.6–40.2 mm SL; same locality; 23 March 2002. – TCWC 13096.10, 20, 20.4–41.7 mm SL; same

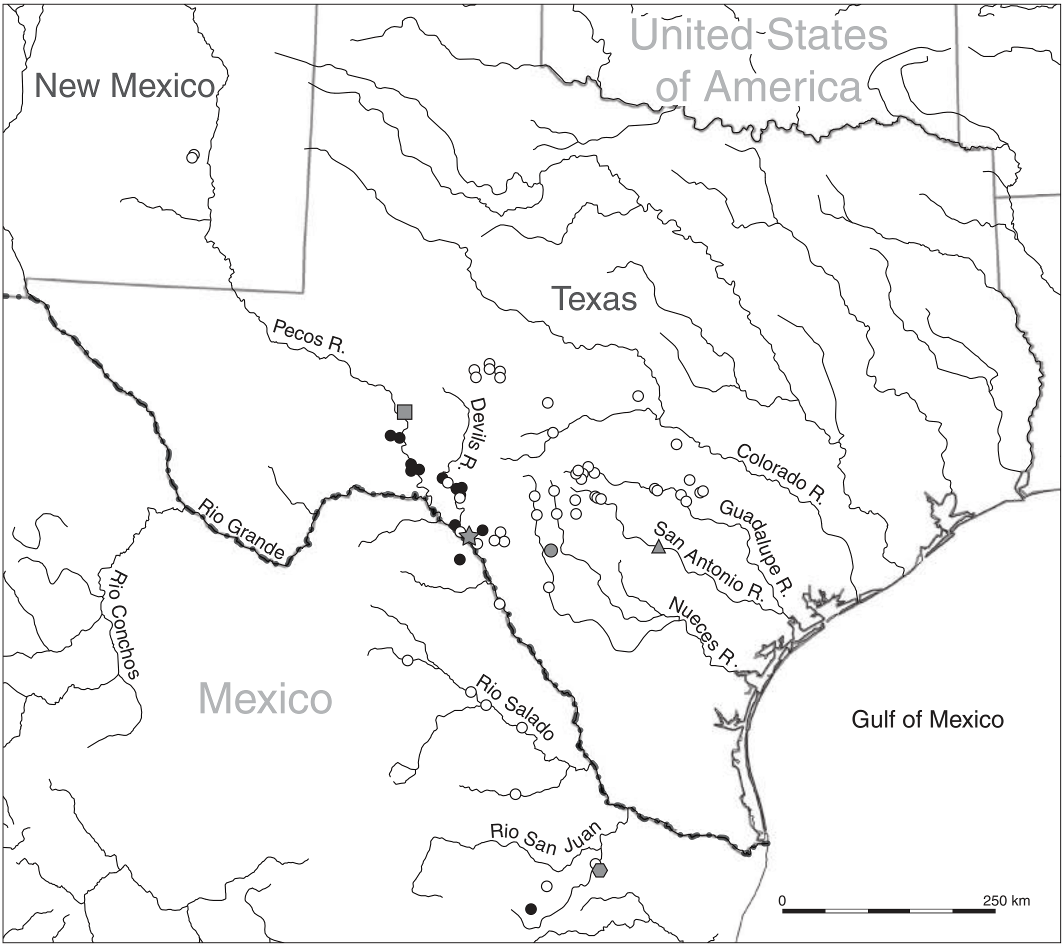

Fig. 10. Distribution of material of *Notropis amabilis* (○) and *N. megalops* (●) examined for this study. Symbols for non-type localities may represent more than one locality. Filled grey symbols represent type localities: *Alburnus amabilis* (●); *A. megalops* (★); *A. socius* (■); *Cyprinella luxiloides* (▲); *C. macrostoma* (⬢).

locality; 3 November 2001. – TCWC 14781.01, 6, 14.0–42.9 mm SL; same locality; 20 May 2001. – TCWC 13084.10, 1, 45.4 mm SL; Val Verde Co.: San Felipe Creek 30 meters upstream from confluence with east spring outflow, 29°22'18''N 100°53'02''W; 21 September 2002. – TCWC 13085.06, 5, 18.4–39.6 mm SL; same locality; 18 January 2003. – TCWC 14774.01, 1, 33.0 mm SL; same locality; 28 April 2001. – TCWC 16455.05, 72, 25.4–47.9; TCWC 16455.06, 28 (DNA vouchers); Val Verde Co.: San Felipe Creek, Academy Street crossing, 29°21'15''N 100°53'45''W; 2 August 2013. – TNHC 27499, 255, 34.6–46.2 mm SL; Val Verde Co.: San Felipe Creek at Canal Street, 29°21'23''N 100°53'41''W; 11 July 1999. – TCWC 1159.01, 63, 20.0–48.7 mm SL; Terrell Co.: Pecos River 28 miles south of Sheffield Chandler Ranch; 9 April 1996. – TCWC 7515.02, 4, 14.5–24.1 mm SL; Terrell Co.: Pecos River; 4 August 1993. – TCWC 7516.06, 20, 21.7–42.7 mm SL; Terrell Co.: Pecos River above confluence with Independence Creek, 30°26'45''N 101°43'14''W; 4 August 1993. – TCWC 7529.04, 1, 43.4 mm SL; same locality; 15 May 1994. – TCWC 3907.07, 11, 29.0–39.0 mm SL; Val Verde Co.: Pecos River 5 miles south of Pandale, 30°07'46''N 101°30'29''W; 27 July 1984. – TCWC 6669.06, 19, 26.6–51.3 mm SL; TCWC 6669.09, 3 (c&s), 43.0–49.0 mm SL; Val Verde Co.: Pecos River 1 mile south of Pandale, 30°09'17''N 101°34'19''W; 28 May 1986. – TCWC 16456.10, 28, 25.7–50.0 mm SL; TCWC 16456.11, 17 (DNA vouchers); Val Verde Co.: Pecos River at Pandale crossing, 30°07'41''N 101°34'23''W; 3 August 2013. – TNHC 15972, 2, 38.3–40.4 mm SL; Val Verde Co.: Pecos River at Pandale crossing, 30°07'41''N 101°34'23''W; 24 May 1988. – TCWC 7513.03, 1, 25.5 mm SL; Terrell Co.: Independence Creek; 15 May 1994. – TCWC 7514.03, 22, 22.0–37.4 mm SL; same locality; 4 August 1993. – TCWC

7515.08, 74, 19.0–45.7 mm SL; same locality; 4 August 1993. – TCWC 7518.04, 5, 40.7–46.6 mm SL; same locality; 15 May 1994. – TCWC 7517.04, 13, 15.0–35.8 mm SL; Terrell Co.: Independence Creek 150 meters upstream from confluence with Pecos River, 30°26'51"N 101°43'28"W; 4 August 1993. – TCWC 7532.04, 18, 26.9–48.9 mm SL; same locality; 15 May 1993. – TCWC 16323.14, 10 (DNA vouchers); TCWC 16323.15, 14, 25.7–37.7 mm SL; Terrell Co.: Independence Creek below bridge crossing on road 349, 30°27'36"N 101°49'30"W; 19 April 2013. – USNM 39654, lectotype of *Alburnus socius*, 55.4 mm SL; USNM 70, 17 paralectotypes of *A. socius*, 42.7–49.5 mm SL, USNM 427772, 1 paralectotype of *A. socius*, 43.5 mm SL; Pecos Co.: Live Oak Creek, east of Sheffield; 1851. – OMNH 65168, 32, 17.9–45.0 mm SL; Val Verde Co.: Devils River at Bakers Crossing, FM 163, 29°58'01"N 101°08'57"W; 27 June 1995. – TCWC 15558.02, 1 (DNA voucher); TCWC 15558.12, 5, 35.0–42.0 mm SL; same locality; 20 November 2011. – TCWC 16325.16, 6, 31.3–47.5 mm SL; same locality; 20 April 2013. – TCWC 16457.02, 2 (DNA vouchers); TCWC 16457.08, 1 (c&s), 33.0 mm SL; same locality; 3 August 2013. – TCWC 7509.07, 46, 21.7–40.2 mm SL; Val Verde Co.: Devils River upstream from Dolan Falls, 29°47'28"N 100°59'28"W; 17 May 1994. – TCWC 7519.04, 1, 36.5 mm SL; same locality; 25 February 1994. – TCWC 7510.09, 44, 25.0–43.0 mm SL; TCWC 7510.11, 3 (c&s), 39.0–44.4 mm SL; Val Verde Co.: Dolan Creek 175 meters upstream from Dolan Falls, 29°53'38"N 100°53'38"W; 3 August 1993. – TCWC 7523.07, 74, 14.4–35.8 mm SL; Val Verde Co.: Devils River, deep pool below Dolan Falls, 29°53'02"N 100°59'38"W; 3 August 1993. – TCWC 7528.02, 22, 22.1–52.8 mm SL; Val Verde Co.: Devils River 150 meters upstream from Dolan Falls, 29°53'26"N 100°59'38"W; 17 May 1994. – TCWC 7533.08, 67, 16.0–41.3 mm SL; Val Verde Co.: Devils River at confluence with Dolan Creek, 29°53'07"N 100°59'36"W; 3 August 1993. – TNHC 16027, 28.4–46.0 mm SL; Val Verde Co.: Devils River Spring; 4 June 1988. – TNHC 58718, 183, 15.0–46.0 mm SL; Val Verde Co.: Devils River; 31 July 2001. – TU 5945, 1, 40.1 mm SL; Val Verde Co.: Devils River near Del Rio at foot of Lake Walk; 17 July 1948. – USNM 129, 3 paralectotypes of *Cyprinella macrostoma*, 33.3–49.5 mm SL: Val Verde Co.: Devils River. – TNHC 29455, 2, 41.2–42.6 mm SL; Val Verde Co., Sycamore Creek, 29°24'32"N 100°42'07"W; 6 June 2002. Mexico: UMMZ 196748, 20 (of 571), 40–44.5 mm SL; Coahuila: Rio San Diego, 27 km south of Ciudad Acuna, 29°5'44"N 100°53'30"W; 1 April 1974. – UAIC 09882.05, 1, 29.7 mm SL; Nuevo Leon: Rio Ramos 5 km west of Allende on Hwy 85, 25°15'38"N 99°59'50"W; 20 July 1990.

Diagnosis. *Notropis megalops* is a member of subgenus *Notropis* (sensu Bielawski & Gold, 2001). It is distinguished from all other members of the subgenus except *N. amabilis* by the following combination of characters: lateral line scales most commonly 36 (range 35–38); circumpeduncle scale rows most commonly 14; predorsal scales most commonly 14 (range 14–17); gill rakers on first gill arch 8–9; anal-fin rays most commonly iii.10 (range iii.10–iii.11); total number of pelvic-fin rays 8 (i.7); total number of vertebrae most commonly 37 (range 37–38); upper arm of ceratobranchial 5 weakly arched; lower lip with dark brown pigmentation; dark lateral stripe well developed. *Notropis megalops* is distinguished from *N. amabilis* by the following combination of characters: body depth greatest at point slightly posterior to insertion of pectoral fins (vs. greatest at point approximately midway between insertion of pectoral and pelvic fins); anterodorsal process of metapterygoid slender and pointed (vs. broad and triangular); dorsal surface of snout and interorbital region of head with black to dark brown pigment arranged as a narrow stripe anteriorly along dorsal midline of snout (vs. uniformly light brown); dark brown stripe along dorsal midline anterior to dorsal-fin origin well developed, widest posteriorly directly anterior to dorsal-fin origin (vs. weakly developed and of uniform width); and anterior portion of lateral line (anterior to vertical through anal-fin origin) disjunct from ventral margin of dark lateral stripe (vs. bordering ventral margin of dark lateral stripe).

Description. General body shape as in Figures 11–13. Morphometric characters are listed in Table 1 and meristic characters in Table 2. Small cyprinid fish, maximum size recorded 52.8 mm SL. Body slightly laterally compressed, fusiform. Dorsal profile weakly arched, rising gradually from snout to dorsal-fin origin, sloping gently towards caudal-fin base. Ventral profile weakly convex anterior to anal-fin origin, weakly concave from anal-fin origin to caudal-fin base. Body depth greatest at point slightly posterior to insertion of pectoral fins; narrowest at midpoint of caudal peduncle. Head and eye relatively large. Pupil elliptical, pointed anteriorly. Mouth large, terminal, posteriormost tip of upper jaw situated below anterior margin of orbit to vertical through anterior margin of pupil. Lips smooth; upper lip notably thicker around anterodorsal margin of upper jaw, obscuring all but anteriormost tip of lower jaw in dorsal view. Snout pointed to weakly rounded, tip located along horizontal through center of pupil to dorsal margin of iris. Nostrils located closer to anterior margin of eye than tip of snout. Anterior nostril small, crescent shaped; separated from larger posterior nostril by low flap of skin. Skin surrounding nostrils and along anterodorsal mar-

Fig. 11. *Notropis megalops*. **a,** *Alburnus megalops,* MCZ 1682, lectotype, 39.7 mm SL; USA: Texas: San Felipe Creek; **b,** *A. socius*, USNM 39654, lectotype, 55.4 mm SL; USA: Texas: Live Oak Creek.

gin of orbit weakly depressed, creating indistinct groove along dorsolateral surface of head, from nostril to horizontal through center of orbit. Gill membranes joined to isthmus anteriorly.

Typically four infraorbital bones (IO1–4). IO1 a flat, elongate rectangular bone, with pronounced projection along dorsal margin. IO2–4 narrow tube-like bones, composed predominantly of sensory canal ossification. IO2 or IO3 divided into two smaller ossifications in few individuals. Cephalic lateral line system well developed; composed of following sensory canals and externally visible pores: infraorbital sensory canal with 10 (1), 11 (2) or 12 (1) pores; supraorbital sensory canal with 7 (2) or 8 (2) pores; preopercular-mandibular sensory canal with 9 (1), 10 (1), 11 (1) or 12 (1) pores (including 4 (2) or 5 (2) in mandibular portion and 5 (1), 6 (2) or 7 (1) in preopercular portion); otic sensory canal with 4 (2) or 5 (2) pores; and temporal sensory canal with 3 pores. Number of pores in cephalic sensory canals frequently asymmetrical. Supraorbital sensory canal with well-developed parietal branch; disjunct from infraorbital and otic sensory canals. Preopercular-mandibular sensory canal terminating along posterior edge of preopercle about midway along vertical arm of bone; disjunct from otic sensory canal.

Pharyngeal teeth 2,4–4,2; slender, unicuspid, with weak dorsally directed distal hook (Fig. 5c–d). Upper arm of ceratobranchial 5 weakly arched (Fig. 5f). Anterior edge of first gill arch with 8–9 slender, dagger-like gill raker ossifications; 6–7 along lower limb, 2 along upper limb. Gill rakers along posterior edge of first gill arch, anterior and posterior edges of second to fourth, and anterior edge of fifth tiny, triangular-shaped bones. Metapterygoid with narrow anterodorsal process bordering posterodorsal edge of endopterygoid (Fig. 6b). Basioccipital process with well developed masticatory plate and pharyngeal process; pharyngeal process rounded posteriorly; terminating directly below 4th vertebral centrum. Hyoid bar with three falciform branchiostegal rays. Basihyal long and slender.

Dorsal-fin rays iii.8 (7). Anal-fin rays iii.10 (5) or iii.11 (2). Principal caudal-fin rays 10 + 9; dorsal procurrent rays 8 (1), 9 (3), 10 (1) or 12 (2); ventral procurrent rays 8 (3), 9 (1), 10 (2) or 11 (1). Pectoral-fin rays i.13 (5) or i.14 (2); pelvic fin rays i.7. Dorsal fin high, triangular with weakly rounded tip; posterior margin straight. Anal fin roughly triangular in shape; posterior margin concave. Anal-fin base longer than dorsal-fin base. Origin of anal fin posterior to vertical line through insertion of last dorsal-fin ray. Caudal fin forked; tip of upper and lower lobes rounded; upper and lower lobes equal in length. Pectoral fin triangular; posterior margin rounded. Pelvic fin small, approximately half of pectoral fin, triangular; posterior margin rounded. Insertion of pelvic fin anterior to vertical line through dorsal-fin origin.

Scales cycloid, large, with few well-developed

Fig. 12. *Notropis megalops*, THNC 27499; USA: Texas: San Felipe Creek; **a,** male, 42.1 mm SL; and **b,** female, 39.6 mm SL.

Fig. 13. *Notropis megalops*, photographed alive; **a,** not preserved, male, ~45.0 mm SL; USA: Texas: Independence Creek; **b,** TCWC 16455.05, female, 39.0 mm SL, USA: Texas: San Felipe Creek.

radii over posterior field of scale body. Lateral line complete, with 35 (1), 36 (19) or 37 (12) or 38 (3) scales, plus 1 (18) or 2 (17) on base of caudal fin. Scales in predorsal scale row 14 (9), 15 (9), 16 (8) or 17 (1). Circumferential scale rows 16 (5), 18 (26) or 20 (2), including 6 (30) or 7 (4) above lateral line and 3 (29) or 4 (5) below lateral line. Circumpeduncular scale rows 12 (14) or 14 (20). Ventral surface between pectoral fins with complete covering of scales. Total number of vertebrae 37 (5) or 38 (2), consisting of 18 + 19 (3), 19 + 18 (2), 19 + 19 (1) or 20 + 18 (1) abdominal and caudal vertebrae.

Small conical tubercles, with pointed tip, irregularly scattered over entire dorsal surface of head, lateral surface of head along dorsal margin of preopercular portion of preopercular sensory canal, and lower jaw in males (Fig. 7b). Scales along dorsal midline between occiput and dorsal-fin origin with irregular scattering of minute conical tubercles in males. Scales on dorsolateral body surface directly posterior to head edged with 4–6 minute conical tubercles in males. Dorsal surface of 8–9 anteriormost pectoral-fin rays with minute conical tubercles, with slightly recurved tip, arranged in regular rows in males (Fig. 8d). Tubercles on dorsal surface of anteriormost pectoral-fin ray arranged predominantly in a single row, with shorter second row present midway along length of ray (Fig. 8e). Tubercles on dorsal surface of second-eight/ninth pectoral-fin rays arranged in multiple rows (Fig. 8f), with number of rows decreasing posteriorly. Females with minute conical tubercles irregularly scattered over dorsal surface of head and lower jaw only.

Coloration. In alcohol, body background colour light cream (Fig. 13). Dorsal surface of head with dark brown stripe, from tip of snout to occiput (Fig. 7b). Thin dark brown stripe along dorsal midline from occiput to caudal fin base, interrupted along base of dorsal fin. Dark brown stripe along dorsal midline most prominent anterior to dorsal-fin origin, expanded laterally into a triangle-like marking directly anterior to dorsal-fin origin (Fig. 9d–f). Narrow dark brown lateral stripe along body side from gill opening to base of caudal fin, continued on posterior half of head by dense scattering of dark brown melanophores over upper half of opercle. Anterior half of lateral stripe on body diffuse, comprised of scattered dark brown melanophores; posterior half of lateral stripe notably darker than anterior half, comprised of densely arranged dark brown melanophores in females and non-tuberculate males. Anterior half of lateral stripe as dark as posterior half and flanked dorsally and ventrally by scattering of small dark brown melanophores in tuberculate males. Scales above lateral stripe edged posteriorly with dark brown melanophores. Scales below lateral line scale row without pigment. Few scattered dark brown melanophores around pore of lateral line canal along first three to five scales in lateral line scale row, around base of anal-fin rays, around ventral margin of eye, lateral surface of snout and upper lip. Ventral surface devoid of pigment except for few scattered melanophores at symphysis of lower jaw. Few dark brown melanophores along branched dorsal-fin rays, densest along shaft ventral to proximalmost fork in rays. Caudal fin with small dark brown melanophores located along length of principal caudal-fin rays. Caudal-fin pigmentation most obvious along two-three outermost and three innermost rays. Small dark brown melanophores along dorsal surface of anteriormost pectoral-fin ray in both sexes and dorsal surface of four to five anteriormost branched pectoral-fin rays in males. Pelvic and anal fins immaculate.

In life, body largely silvery with pale brown to straw colored dorsal surface (Fig. 13). Dorsal surface of eyes and occiput with green sheen. Dark brown stripe running along dorsal surface of head distinct. Lateral stripe indistinct, bordered dorsally by a thin golden stripe. Dark brown melanophores around posterior edge of scales dorsal to lateral stripe distinct, forming obvious reticulate pattern over dorsal surface of body. Dorsal midline with green-golden stripe, most obvious anterior to dorsal fin. Dark brown line running along dorsal midline visible anterior to dorsal-fin origin as a dark brown pre-dorsal spot. Scales in third scale row along side of body with small patch of blue iridiophores at center, forming series of indistinct blue spots along upper side of body, most obvious along posterior half of body in dorsal view (Fig. 16b). Pectoral fins with yellow hue in tuberculate males. Dark brown pigmentation on fins indistinct.

Distribution. *Notropis megalops* is endemic to the Rio Grande drainage of the United States (Texas) and Mexico (Coahuila and Nuevo Leon) (Fig. 10). Within the United States, *N. megalops* is abundant within San Felipe Creek, the lower portion of the Pecos River (between the confluence with Independence Creek and the Rio Grande) and Independence Creek, and sporadically distributed throughout the Devils River. We have also examined two individuals of *N. megalops* from Sycamore Creek, a small, spring-fed north bank tributary of the Rio Grande east of the city of Del Rio (Val Verde County, Texas). We have examined relatively few specimens of *N. megalops* from the Mexican portion of the Rio Grande drainage, including specimens from the Rio San Diego, a south bank tributary of the Rio Grande (Coahuila), and a single individual from the Rio Ramos at the headwaters of the Rio San Juan (Nuevo Leon). We expect *N. megalops* is also present in the Rio Salado but lack material from this Mexican tributary to the Rio Grande.

Notropis megalops is abundant throughout San Felipe Creek in the City of Del Rio, which is listed as the type locality for *Alburnus megalops* by Girard (1858). Girard (1858) reported the type locality of *A. socius* as Live Oak Creek, 8 miles west of the town of Sheffield, Texas. Our recent sampling efforts throughout Live Oak Creek failed to produce individuals of *N. megalops*.

Comparative morphology

***Notropis amabilis* and *N. megalops*.** *Notropis amabilis* and *N. megalops* are similar in general appearance and exhibit overlapping values for all meristic characters and proportional measurements that we have examined as part of this study. The general similarity between proportional measurements obtained from examined specimens of *N. amabilis* and *N. megalops* is echoed in the scatterplots derived from the size corrected PCA (Fig. 14), in which both species exhibit overlap and do not separate along the major dimensions. A MANOVA of the PC axes contributing to 95 % of the cumulative variance (PC1–14) revealed a significant difference between *N. amabilis* and *N. megalops* ($F[15,63] = 8.82$, $P < 10^{-9}$), though the effect was modest ($\eta^2 = 0.68$), confirming the overlap in major PC dimensions.

Contrary to the overlap in quantitative characters, *N. amabilis* and *N. megalops* exhibit a number of differences in colour pattern, including aspects of both dorsal and lateral pigmentation. The most striking pigmentation difference between *N. amabilis* and *N. megalops* is undoubtedly the arrangement of dark brown or black melanophores over the anterodorsal surface of the head. In *N. amabilis* the anterodorsal surface of the head, from the tip of the snout to the point through the anterior margin of the orbit is sparsely populated with melanophores (Fig. 7a). In *N. megalops* this region of the head is densely populated with melanophores (Fig. 7b), which are confluent with the field of melanophores located on the dorsal surface of the head between the orbits. This arrangement of melanophores in *N. megalops* contributes to a short, but distinct, black to dark brown stripe along the dorsal surface of the head, extending from the tip of the snout to the occiput (Figs. 7b, 13b). The dark stripe along the dorsal midline of the body, anterior to the dorsal-fin origin, represents another difference between *N. amabilis* and *N. megalops*. In *N. amabilis*, this stripe is relatively uniform in thickness along its length (Fig. 9c) whereas in *N. megalops* this stripe is obviously thicker posteriorly, where it is expanded laterally to form a triangular marking (Fig. 9f). This difference is present even in smaller individuals (≥25.0 mm SL) and represents a useful character for distinguishing between juveniles of *N. amabilis* and *N. megalops*, especially at localities where both occur in sympatry (e.g., Devils River, Texas).

The relationship between the dark lateral stripe present along the side of the body and the lateral line represents another difference between *N. amabilis* and *N. megalops*. In *N. amabilis*, the anterior half of this stripe (from posterior to the opercular opening to the point located on the vertical through the anal-fin origin) is bordered ventrally by the lateral line (i.e., the lateral line is in contact with the dark lateral stripe along the entire length of the body). In *N. megalops* the dark lateral stripe is disjunct from the lateral line along most of the anterior half of the body and the two are in contact only at the anteriormost part of the body (just posterior to the opercular opening) and along the posterior part of the body (posterior to the vertical through the anal-fin origin). We are undecided whether this difference is the result of differences in the composition of the dark lateral stripe, the path of the lateral line canal along the body side or a combination of both.

We have identified only a single consistent osteological difference between *N. amabilis* and *N. megalops* relating to the shape of the metapterygoid of the hyopalatine arch. In *N. amabilis* the anterodorsal process of metapterygoid is broad and triangular (Fig. 6a) compared to slender and pointed in *N. megalops* (Fig. 6b). Tuberculation of *N. amabilis* is generally similar to that of *N. megalops* (e.g., see Fig. 8) and we have been unable to identify a single consistent difference between the two species in this character complex.

***Notropis jemezanus*.** During the course of our study we became aware of several collections of *N. amabilis* and *N. megalops* that have been incorrectly identified as *N. jemezanus* and we take this

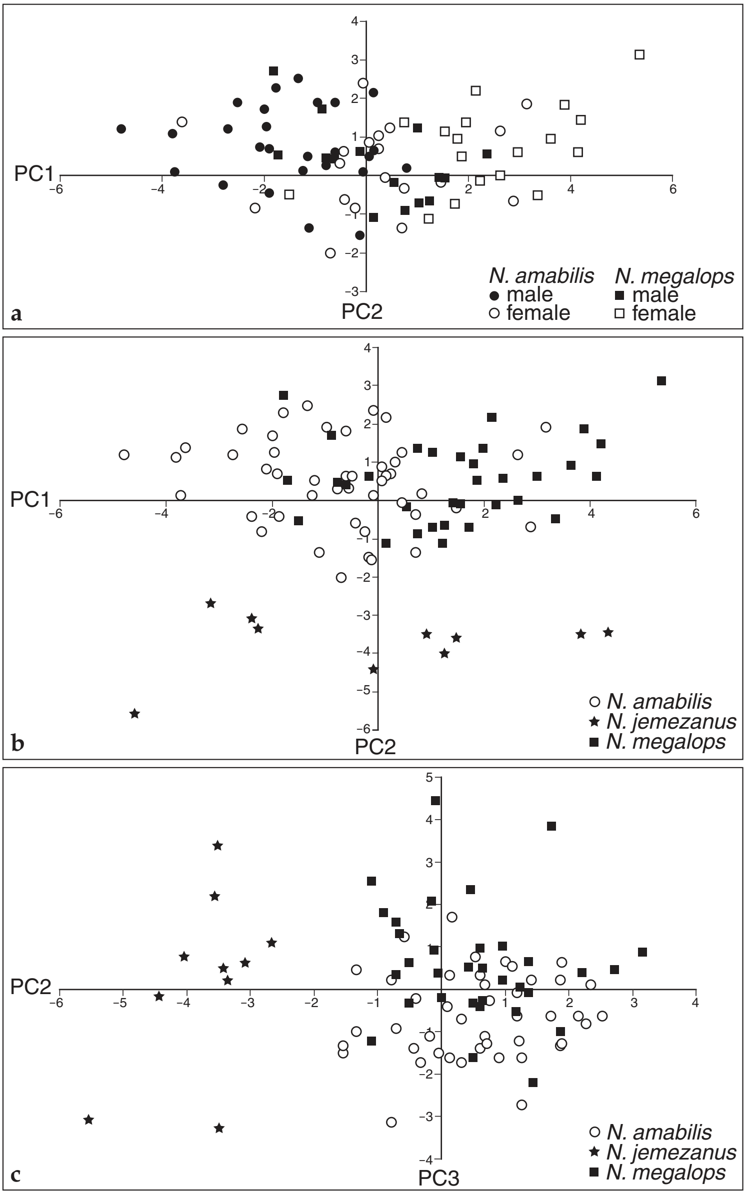

Fig. 14. PCA scatter of the size corrected morphometric data for 79 specimens representing 3 species of the subgenus *Notropis*, including *N. amabilis* (40), *N. jemezanus* (10) and *N. megalops* (29). **a,** PC1 plotted against PC2 for *N. amabilis* and *N. megalops* with different sexes identified with filled (male) or open (female) symbols. **b,** PC1 plotted against PC2 for *N. amabilis*, *N. jemezanus* and *N. megalops* (sexes not distinguished). **c,** PC2 plotted against PC3 for *N. amabilis*, *N. jemezanus* and *N. megalops* (sexes not distinguished).

opportunity to briefly point out the main differences between these species here.

The proportional measurements that appear to be most useful for distinguishing between *N. jemezanus* and *N. amabilis*/*N. megalops* amongst those that we have examined include the diameter of the orbit, which is lesser in *N. jemezanus* (19–27 % HL) compared to the other two species (29–36 % HL), and the distance between the snout and the dorsal-fin origin (pre-dorsal distance), which is slightly longer in *N. jemezanus* (53–57 % SL) compared to the other two species (49–55 % SL). In the scatterplots resulting from the PCA of the size corrected morphometric data, *N. jemezanus* is well separated from *N. amabilis* / *N. megalops* (Fig. 14b–c) based on both orbit diameter and pre-dorsal distance, in addition to other measurements of the head (head length, head depth at orbit, head depth at occiput) and body (pre-dorsal length, length of caudal peduncle) (Table 3). Thomas et al. (2007) also reported the length of the pelvic fin in *N. jemezanus* to be shorter than that of *N. amabilis* (including *N. megalops*), a difference that we can confirm (qualitatively but not quantitatively) from our material (tip of depressed pelvic fin not reaching anus in *N. jemezanus* vs. extending past anus in *N. amabilis* and *N. megalops*). *Notropis jemezanus* also appears to reach a much greater body size than either *N. amabilis* or *N. megalops*. The largest individual of *N. jemezanus* that we examined was 68.5 mm SL compared to 58.5 and 52.8 in *N. amabilis* and *N. megalops*, respectively.

The slightly longer pre-dorsal distance in *N. jemezanus* compared to *N. amabilis* / *N. megalops* is reflected in differences in the number of abdominal vertebrae and the insertion of the first dorsal-fin pterygiophore. Though the total number of vertebral centra is similar in all three species (38–39 in *N. jemezanus*, 36–38 in *N. amabilis*, 37–38 in *N. megalops*), *N. jemezanus* has a higher number of abdominal centra (21) than either *N. amabilis* (17–19) or *N. megalops* (17–20). The insertion of the first dorsal-fin pterygiophore is also located further caudally in *N. jemezanus* (between neural spines of vertebral centra 14/15) compared to either *N. amabilis* or *N. megalops* (11–13/12–14). *Notropis jemezanus* also exhibits a greater number of ribs than either *N. amabilis* or *N. megalops* (16 in *N. jemezanus* vs. 13–14 in both *N. amabilis* and *N. megalops*). Taken together, these differences may suggest that *N. jemezanus* possess a slightly longer abdominal cavity than either *N. amabilis* or *N. megalops*. In addition to differences in the vertebral and median fin skeleton, *N. jemezanus* differs also from *N. amabilis* and *N. megalops* in aspects of the splanchnocranial skeleton. In *N. jemezanus*, the upper arm of the fifth ceratobranchial (cb5) is strongly arched (Fig. 5g) compared to only weakly arched in both *N. amabilis* and *N. megalops* (Fig. 5e–f). As in *N. megalops*, the anterodorsal process of the metapterygoid is slender and pointed in *N. jemezanus* (Fig. 6c) compared to broad and triangular in *N. amabilis* (Fig. 6a).

Table 3. Variable loadings on size-corrected principal components 1–3 from analysis of reduced morphometric data set comprising *Notropis amabilis* (n = 40), *N. megalops* (n = 29) and *N. jemezanus* (n = 10). Highest loadings in bold.

	PC 1	PC 2	PC 3
Body depth	0.201	−0.113	0.076
Pre-dorsal length	0.054	**−0.423**	−0.139
Pre-pelvic length	0.233	−0.037	**−0.435**
Pre-anal length	0.104	−0.304	−0.341
Pre-anus length	0.048	−0.159	−0.260
Base of dorsal fin	0.075	−0.128	**0.477**
Base of anal fin	−0.007	−0.226	**0.459**
Dorsal-caudal length	0.057	0.312	0.200
Length of caudal peduncle	−0.089	**0.448**	−0.050
Depth of caudal peduncle	0.066	−0.138	0.209
Head Length	**0.377**	0.114	−0.072
Head depth at orbit	**0.374**	0.126	0.019
Head depth at occiput	**0.377**	−0.027	0.089
Orbit Diameter	0.197	**0.418**	−0.037
Interorbital width	0.041	−0.006	0.209
Snout length	0.266	−0.208	0.096
Snout to occiput	0.335	0.208	−0.022
Mouth width	0.305	−0.109	0.054
Length of lower jaw	**0.356**	−0.030	0.085
Eigenvalue	5.135	3.113	2.162
Cumulative Variance %	27.0	43.4	54.8

Phylogenetic analyses

MP and ML analyses of the cyt b (Fig. 15) and RAG 1 (Fig. 16a) data sets and Bayesian analysis of the concatenated three-gene data set (Fig. 16c) resulted in a monophyletic grouping comprising all members of the subgenus *Notropis* included herein (viz. *N. amabilis*, *N. atherinoides*, *N. jemezanus*, *N. megalops*, *N. percobromus* and *N. stilbius*). MP and ML analyses of the S7 data set recovered members of the subgenus *Notropis* together with *P. vigilax* (Fig. 16b), though this grouping did

Table 4. Means of corrected genetic distances within and between *Notropis amabilis* (n = 69), *N. megalops* (n = 41) and *N. jemezanus* (n = 2) for a 1137 bp fragment of the cyt *b* gene.

	N. amabilis	*N. megalops*	*N. jemezanus*
N. amabilis	0.02554883	–	–
N. megalops	0.140971087	0.008965211	–
N. jemezanus	0.079877	0.15087092	0.00616

not receive bootstrap support. The relationships between members of the subgenus *Notropis* depicted in the topologies resulting from the different analyses of the individual gene data sets are conflicting but we note here that *N. megalops* and *N. amabilis* are never recovered in a sister group relationship. In the topologies resulting from the MP and ML analyses of the cyt *b* (Fig. 15) and RAG 1 data sets (Fig. 16a; ML topology not shown), *N. megalops* is the sister group to all remaining members of the subgenus *Notropis*. Within these topologies *N. amabilis* is the sister group to either *N. jemezanus* (MP and ML analyses of cyt *b* [without bootstrap support]; Fig. 15) or the sister group to a clade including *N. atherinoides*, *N. jemezanus* and *N. percobromus* (MP and ML analyses of RAG 1 [with weak bootstrap support]; Fig. 16a). In the topologies resulting from the MP and ML analyses of the S7 data set, *N. amabilis* is the sister group to all remaining members of the subgenus *Notropis* excluding *N. megalops* (Fig. 16b; ML topology not shown). In the topology resulting from the Bayesian analysis of the concatenated data set, *N. megalops* is the sister group to all remaining members of the subgenus *Notropis* and *N. amabilis* is the sister group to *N. jemezanus* plus *N. stilbius* (Fig. 16c).

For the segment of cyt *b* gene investigated, the uncorrected p-distance between *N. amabilis* and *N. megalops* is 14.1 % (Table 1). For comparison, the uncorrected p-distance between the putative sister taxon pair of *N. amabilis* and *N. jemezanus* based on evidence from the cyt *b* gene (Bielawski & Gold, 2001; Schönhuth & Doardio, 2003; Fig. 15) is 8.0 % (Table 1). The uncorrected p-distance for the same cyt *b* fragment within *N. amabilis* and *N. megalops* is 2.5 % and 0.8 %, respectively (Table 1).

Discussion

Synonymy of *Notropis amabilis* and *N. megalops*. Several of the species described by Girard (1856) have been placed or tentatively placed in the synonymy of *N. amabilis* (= *Alburnus amabilis* of Girard), including *A. megalops*, *A. socius*, *Cyprinella macrostoma* and *C. luxiloides* (reviewed by Gilbert, 1978, 1998). The last occasion on which all five of these nominal taxa were considered valid appears to be Girard (1859), in which the three species he had earlier included in *Alburnus* (*A. amabilis*, *A. megalops* and *A. socius*) were listed instead as members of the genus *Alburnellus*. In their treatise of North American fishes, Jordan & Gilbert (1883) considered *N. amabilis* as valid (without synonyms; p. 195), *N. megalops* as valid (with *A. socius* as a junior synonym; p. 195) and *C. macrostoma* as valid (with *C. luxiloides* as a junior synonym; p. 177), though later, Jordan (1885) considered *A. megalops* and *A. socius* as distinct and together with Gilbert (Jordan & Gilbert, in Jordan, 1885: 123) introduced the replacement name *Notropis swaini* for *A. megalops* (discussed below). Subsequent to Jordan (1885), *N. swaini* appears to have been considered valid only by Jordan & Evermann (1896: 290) and Baughman (1950) and appears to have been first placed in the synonymy of *N. amabilis* by Hubbs et al. (1953). Hubbs et al. (1953) considered *C. luxiloides* as a subspecies of *Cyprinella lutrensis* and separate from *C. macrostoma*, which Miller (1976) placed in the synonymy of *N. amabilis*. In his type catalogue of the North American cyprinid genus *Notropis*, Gilbert (1978) listed *A. megalops* (including the replacement name *N. swaini*), *A. socius* and *C. macrostoma* in the synonymy of *N. amabilis* and indicated that *C. luxiloides* was also “probably” a synonym of *N. amabilis* (as did Gilbert, 1998).

We have shown, based on a combination of morphological and molecular evidence, that *N. amabilis* as recognized in recent ichthyological works (e. g., Lee et al., 1980; Miller, 2005; Thomas et al., 2007; Hubbs et al., 2008; Hendrickson & Cohen, 2015) comprises two separate species. One of these species is widespread throughout the drainages traversing the Edwards Plateau of Texas (Brazos, Colorado, Guadalupe, San Antonio and Nueces drainages) and the Rio Grande drainage of the United States (Texas and New Mexico) and Mexico; the name *N. amabilis* is retained for this species (see below). The other species is restricted to the Rio Grande drainage of the United States (Texas) and Mexico (Fig. 10); the name *N. megalops* is retained for this species (see below).

Unfortunately, Girard’s (1856) original description of *A. amabilis* and his descriptions of the four species currently placed or tentatively placed in its synonymy (viz. *A. megalops*, *A. socius*, *C. macrostoma* and *C. luxiloides*; Gilbert, 1978, 1998) are brief and do not contain characters that would be useful for distinguishing between them. The condition of the type material for each of these species ranges from fair (*A. amabilis*, *A. megalops* and *C. macrostoma*) to extremely poor (*A. socius* and *C. macrostoma*) or has been lost (*C. luxiloides*)

(Gilbert, 1978, 1998) and is of little use for distinguishing between these nominal species.

The type series of *N. amabilis* includes 29 syntypes (Gilbert, 1978) from a single locality (Río Leona near Uvalde, Uvalde County, Texas; Girard, 1856). We have examined only 26 of the 29 (USNM material only). USNM 72, 50.3 mm SL (Fig. 2a) is the largest of the syntypes that we have examined that exhibits all of the characters listed above as diagnostic for *N. amabilis*; it is here designated as lectotype of *N. amabilis*. The remaining syntypes from USNM (USNM 427771) all belong to *N. amabilis*.

The type series of *N. megalops* includes five syntypes (Gilbert, 1998), from a single locality (San Felipe Creek near Del Rio, Val Verde County, Texas; Girard, 1856). We have examined only two of the five (MCZ material only). MCZ 1682, 39.7 mm SL (Fig. 11a) is the largest of the two syntypes and it exhibits all of the characters listed above in the diagnosis for *N. megalops*; it is here designated as lectotype of *N. megalops*. The remaining syntype from MCZ (now MCZ 171862) belongs to *N. megalops*.

The existing type series for *Alburnus socius* comprises 25 specimens (Gilbert, 1998) from a single locality (Live Oak creek, Crockett County, Texas; Girard, 1856). We have examined only 23 of the 25 (USNM material only). They belong to two different species: *N. megalops* (USNM 70 [17 specimens], 39654 [1 specimen], and 427772 [1 specimen]) and *Dionda argentosa* (USNM 344866, 1 specimen). Gilbert (1998) noted that the specimen of *D. argentosa* (referred to as *Notropis volucellus*) in USNM 344866 was previously part of USNM 70. This specimen may have been separated from the reminder of the syntypes contained within USNM 70 because it was earlier recognized as different by an unidentified examiner (J. Williams, pers. comm.). Despite this separation, the individual of *D. argentosa* remains part of the syntype series of *A. socius* and to definitively link the name to one of the two species, we designate USNM 39654, 55.4 mm SL (Fig. 11b) as lectotype of *A. socius*. This individual shows all the characters diagnostic for *N. megalops* listed above and this makes *A. socius* a subjective simultaneous synonym of *A. megalops*. Jordan & Gilbert (1883: 195) acted as first reviser and gave precedence to *N. megalops* when they listed *A. socius* as its synonym.

The type series of *Cyprinella macrostoma* comprises material from two different localities within the Rio Grande drainage (Girard, 1856), including three specimens from the United States (Devils River, Val Verde County, Texas; USNM 129), and two from Mexico (Rio San Juan, near China, Nuevo Leon; MCZ 1798 [Fig. 1b], MNHN 0000-0371). The syntypes for *C. macrostoma* that we have examined (all but MNHN specimen) comprises a single large (45.5 mm SL) specimen that is in fairly good condition (MCZ 1798) and three specimens that are in very poor condition (USNM 129), including one larger specimen (49.5 mm SL) and two smaller specimens (33.5, 35.0 mm SL). The specimen from the Rio San Juan (MCZ 1798) exhibits a number of characters of *N. amabilis* (dorsal surface of head between snout uniformly pigmented, anterodorsal process of metapterygoid broad and triangular [confirmed via ct scan]) and does not exhibit characters of *N. megalops* and we are confident that this specimen belongs to *N. amabilis*. The specimens from the Devils River are similar to both *N. amabilis* and *N. megalops* in general appearance but due to their poor condition we are unable to identify them as belonging to either species with any certainty. Given that both *N. amabilis* and *N. megalops* are sympatric within the Devils River it is possible (though we are unable to confirm) that USNM 129 may be a mixed lot, comprising individuals of both *N. amabilis* and *N. megalops*. In order to fix the status of *C. macrostoma* we designate MCZ 1798, 45.5 mm SL (Fig. 2a) as lectotype. This specimen belongs to *N. amabilis* and this renders *C. macrostoma* a subjective simultaneous synonym of *A. amabilis*. Miller (1976) listed *C. macrostoma* as a junior synonym of *N. amabilis* and this way acted as first reviser and gave precedence to *N. amabilis*.

Girard (1856) described *Cyprinella luxiloides* based on two specimens (USNM 131) collected from San Pedro Creek, a tributary to the San Antonio River (Bexar County, Texas). The syntypes of *C. luxiloides* are no longer extant (Gilbert, 1978, 1998) but illustrations in Girard (1859: pl. 31, figs 13–16; reproduced here in Fig. 1) were considered by Gilbert (1998: 108) to be derived from type material. Though Gilbert (1978) was uncertain about the identity of *C. luxiloides*, he tentatively placed this species in the synonymy of *N. amabilis*, based largely on the views of earlier authors (i. e., Jordan & Gilbert [1883: 177] considered *C. luxiloides* a synonym of *C. macrostoma*, which Gilbert [1978] considered a synonym of *N. amabilis*) and a similarity between Girard's (1859) illustrations of *C. luxiloides*, *C. macrostoma* and *N. amabilis*. Though we agree with Gilbert (1978) that Girard's

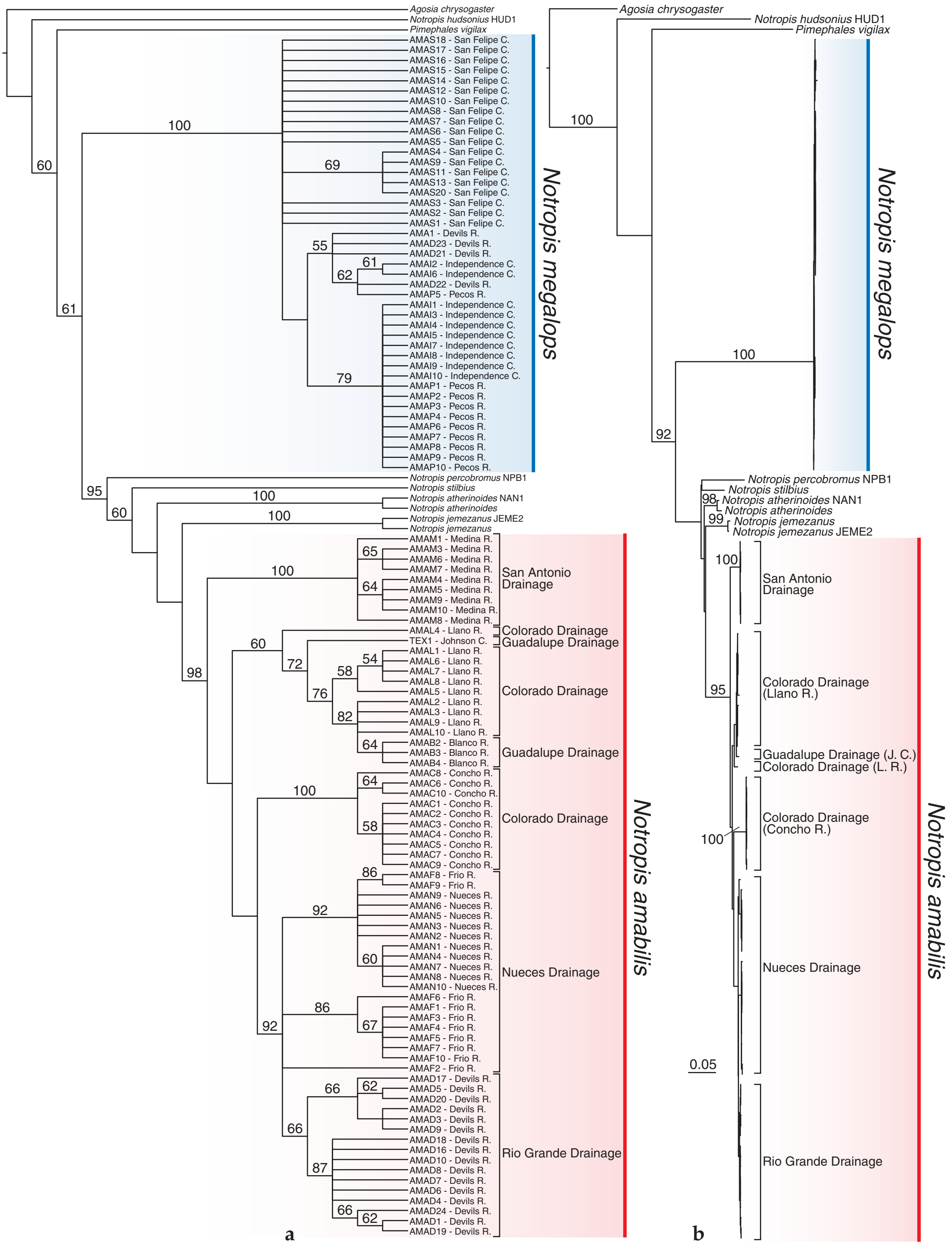

Fig 15. Phylogenetic trees derived from MP and ML analyses of cyt *b* data set. **a,** strict consensus of 15 equally parsimonious cladograms (900 steps; CI = 0.54; RI = 0.95) derived from MP analysis; **b,** maximum likelihood phylogram (–ln *L* 5442.67306). Numbers above branches represent bootstrap support values in both a and b.

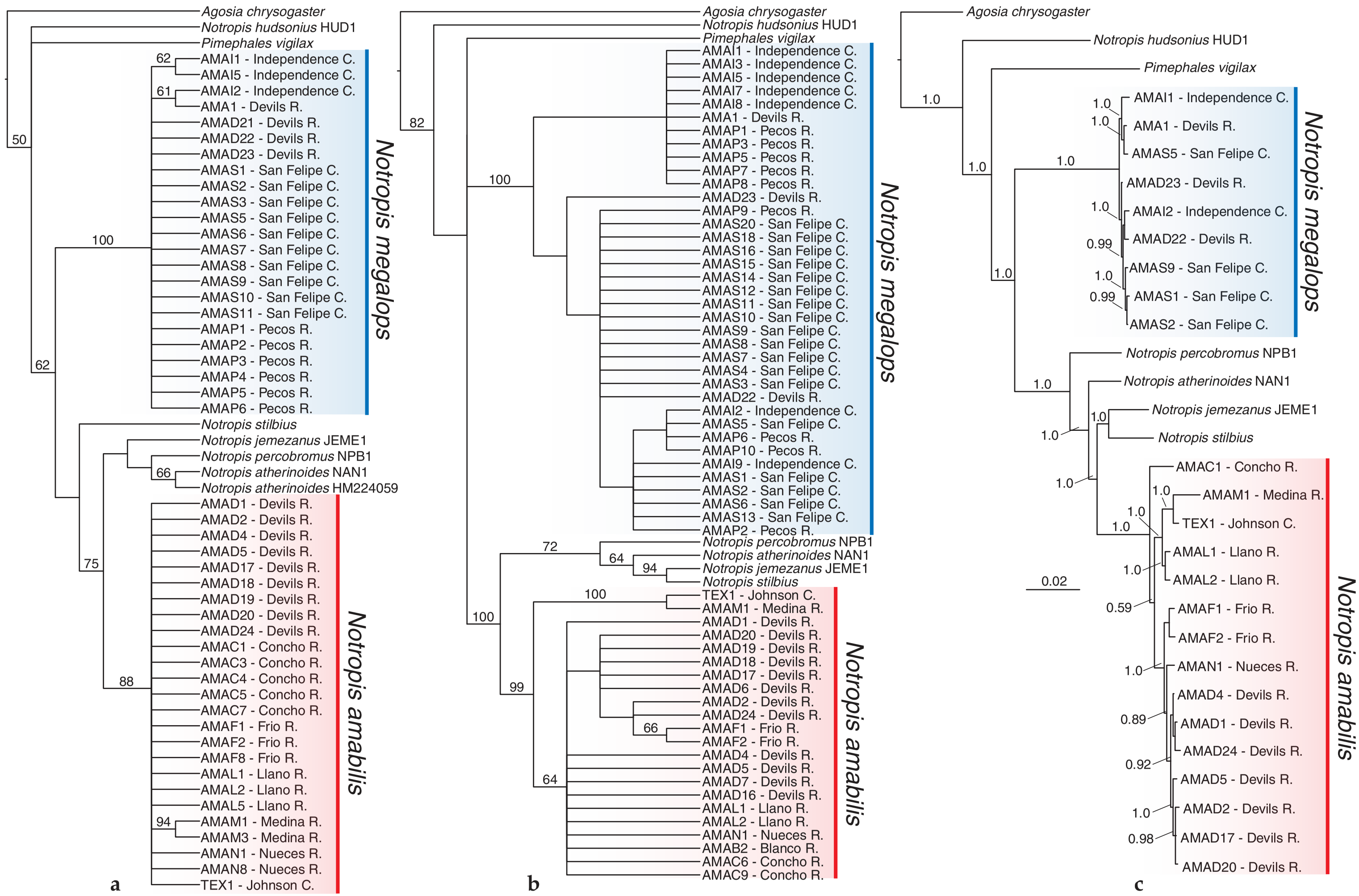

Fig 16. Phylogenetic trees derived from MP and Bayesian analyses of nuclear genes and combined dataset. **a,** strict consensus of 3460 equally parsimonious cladograms (130 steps; CI = 0.83 ; RI = 0.90) derived from parsimony analysis of RAG 1 data set; **b,** strict consensus of 12210 equally parsimonious cladograms (257 steps; CI = 0.85; RI = 0.97) derived from parsimony analysis of S7 data set; **c,** phylogenetic tree derived from the partitioned Bayesian analysis of the combined data set. Numbers above branches represent bootstrap support values (a and b) or posterior probabilities (c).

(1859) illustrations of *C. luxiloides* and *C. macrostoma* are similar, we consider Girard's (1859) illustrations of *N. amabilis* to be very different from those provided for *C. luxiloides*, especially in terms of overall body shape and head shape (compare Fig. 1a with Fig 1e). Contrary to Gilbert (1978), we consider Girard's illustration of *C. luxiloides* to bear a stronger resemblance (based on body and head shape) to *Cyprinella lutrensis* (Baird & Girard, 1853) than to *N. amabilis*. Hubbs et al. (1953) listed *C. luxiloides* as a subspecies of *C. lutrensis*, though without explanation, suggesting that they also considered *C. luxiloides* to have more in common with *C. lutrensis* than *N. amabilis*. Both *N. amabilis* and *C. lutrensis* are present at the type locality of *C. luxiloides* (Hendrickson & Cohen, 2015) and we consider the designation of a neotype nessecary in order to clarify the identify of *C. luxiloides*. We select TCWC 14075.01, 51.0 mm SL (Fig. 17) as neotype for *C. luxiloides*. We have selected this specimen because it matches well with the illustration of the suspected (Gilbert, 1998: 108) type material of *C. luxiloides* provided in Girard (1856: pl. 31, figs. 13–16 [reproduced in Fig. 1]) and was collected close to the type locality (San Antonio River, Bexar County, Texas). This specimen belongs to *C. lutrensis,* rendering *C. luxiloides* a junior synonym of *C. lutrensis*

Jordan & Gilbert (in Jordan, 1885: 123) introduced the replacement name *Notropis swaini* for *A. megalops* Girard, 1856 because they considered that the specific name *megalops* was preoccupied in *Notropis* by *Cyprinus megalops* Rafinesque, 1817. These would have been secondary homonyms in today's International Code of Zoological Nomenclature (ICZN). Indeed *C. megalops* Rafinesque, 1817 was then placed in *Notropis* but as a synonym of *N. cornutus* (Mitchill, 1817) (now *Luxilus cornutus*; Gilbert, 1968), not as a valid species of *Notropis*. The name *megalops* of Rafinesque does not appear to have ever been used as the valid name for a valid species in the combination *Notropis megalops* and therefore there is no secondary homonymy (ICZN art. 57.3.1), thus the replacement name *N. swaini* was not justified and it is a mere junior objective synonym of *A. megalops*.

Distribution of *Notropis amabilis* and *N. megalops*. Miller (2005), Hubbs et al. (2008) and Page & Burr (2011) provide the most recent overviews of geographic distribution for *N. amabilis* (all inclusive of *N. megalops*). Miller (2005) considered *N. amabilis* to occur "from the Colorado River of central Texas southward into the Río Bravo [Rio Grande] basin, including ríos Salado and San Juan, COAH, NLE, TAM [Coahuila, Nuevo Leon, Tamaulipas], westward to the Pecos River, TX, NM [Texas, New Mexico], and Rio Conchos, CHIH [Chihuahua]." Hubbs et al. (2008) described the distribution of *N. amabilis* as "primarily within the Edwards Plateau streams (including portions of the San Gabriel River [Brazos drainage] on the northeast) and to the Pecos River in the west. The species is also found in Rio Grande tributaries in Mexico, including the Río Salado and Río San Juan". The recognition of *N. megalops* as a valid species necessitates only minor revision to the distribution of *N. amabilis*. Using Miller's (2005) summary distribution as a template, and based only on the material we have examined (Fig. 10), *N. amabilis* occurs from the Colorado River drainage of central Texas southward into the Rio Grande drainage, including the Río Salado and Río San Juan, westward to the Devils River (Texas), with a highly disjunct and reportedly extirpated (Sublette et al., 1990) population in the upper Pecos River basin around Roswell (New Mexico). Based on the material that we have examined, *N. amabilis* should no longer be considered to occur in the lower Pecos River basin in Texas. All previous records of *N. amabilis* from this part of the Rio Grande drainage (e. g., Hoagstrom, 2003; Bonner et al., 2005; Hubbs et al. 2008; Hendrickson & Cohen, 2015) most probably refer to *N. megalops*. Miller (2005) also considered *N. amabilis* to be present in the Río Conchos (Chihuahua, Mexico) but did not include localities within this basin in his distribution map for *N. amabilis* within Mexico (Miller, 2005: map 6.84, p. 132) nor is the Río Conchos incorporated into the summary distribution for this species (map 6.84 inset, p. 132). *Notropis amabilis* was not listed as a component of the Río Conchos ichthyofauna by Edwards et al. (2002, 2003) and, contrary to Miller (2005), we suspect that *N. amabilis* may be absent from this westernmost part of the Rio Grande drainage. The single lot of *N. amabilis* that we have examined from the main stem of the Rio Grande (TNHC 24680) appears to be atypical as the majority of our material hails from smaller creeks and rivers that are heavily influenced by spring flows. We note, however, that *N. amabilis* has also been reported from the lower Rio Grande by Edwards & Contreras-Balderas (1991) and by Hendrickson & Cohen (2015). *Notropis amabilis* has been also reported from the San Gabriel River of central Texas (Hubbs et al., 2008; Hendrickson & Cohen, 2015) suggesting that the distribution of this species may extend north of the Colorado River drainage and into the Brazos River drainage at least along the northeastern border of the Edwards Plateau.

Notropis megalops was originally described by Girard (1856) based on specimens from San Felipe Creek (Val Verde Co., Texas). Based solely on material that we have examined (Fig. 10), we consider the distribution of *N. megalops* to be restricted entirely to the lower Rio Grande drainage, including both north (United States) and south (Mexico) bank tributaries of the Rio Grande from the Pecos River eastwards to Sycamore Creek (Kinney Co., Texas) and the Río San Diego (Coahuila), with a putatively disjunct population in the headwaters of the Río San Juan (Río Ramos, Nuevo Leon, Mexico). This disjunct distribution may be an artifact of our limited material from the Río San Juan and Río Salado and further survey work within each of these basins should help to refine the distribution of *N. megalops* within the Mexican states of Coahuila and Nuevo Leon. If shown to occur within the Río Salado, the distribution of *N. megalops* would closely match that of two other Rio Grande endemics, *Cyprinella proserpina* and *Etheostoma grahami* (Miller, 2005).

Despite broadly overlapping distributions within the Rio Grande drainage, *N. amabilis* and *N. megalops* do not appear to co-occur often. Through our own field-work in the United States we have collected *N. amabilis* and *N. megalops* together only at a single location on the Devils River (Bakers Crossing, Val Verde Co., Texas) and have examined older collections containing both species from further downstream on the same river (immediately upstream and downstream of Dolan Falls). The only other water body from which we have examined material of both species (though from separate locations) is Sycamore Creek (Kinney/Val Verde Co., Texas), a small northbank tributary to the Rio Grande. It is unclear, based on the material that we have examined, whether *N. amabilis* and *N. megalops* occur sympatrically within the Mexican portions of their distributions.

Unfortunately, our efforts to collect *N. amabilis* and *N. megalops* from several localities at which *N. amabilis* (inclusive of *N. megalops*) had been recorded previously within south central Texas were unproductive, including sites within Los Moras Creek (Robinson, 1959), Pinto Creek (Garrett et al., 2004), the Leona River (type locality of *A. amabilis*; Girard, 1856), the Sabinal River (Hendrickson & Cohen, 2015), and Live Oak Creek (type locality of *A. socius*; Girard, 1856). Deciphering whether the absence of *N. amabilis* and/or *N. megalops* from these localities is real or an artifact of our inability to sample broadly within these water bodies will require further survey work within this region of the southern United States. Extirpation and extinction is a reality for freshwater fishes throughout the Rio Grande drainage of North America, especially cyprinids (Miller et al., 1989; Hubbs, 1990; Bestgen & Platania, 1990, 1991; Edwards et al., 2002, 2003), and the disappearance of *N. amabilis* from the periphery of its range within the Rio Grande in both the United States (upper Pecos River basin, New Mexico; Sublette et al., 1990) and Mexico (Río San Juan, Nuevo Leon; Contreras-Balderas, 1975; C. Villarreal-Treviño [unpub. Ph.D. dissertation] in Villarreal-Treviño et al., 1986) should serve as a warning that this species is not immune to the factors driving the decline of freshwater fishes generally within this imperiled system. Perhaps the saving grace for *N. amabilis* is that the core of its distribution is located to the north of the Rio Grande, including the Gulf Coast drainages traversing the Edwards Plateau of central Texas from the Colorado southwards to the Nueces. The same cannot be said for the Rio Grande endemic *N. megalops*, which with an already highly fragmented distribution combined with low levels of intraspecific variation at least in the fragment of the cyt *b* gene that we have investigated (uncorrected p-distance 0.08 %), should be considered a future priority for conservation.

Conclusions

We have shown, based on a combination of morphological and molecular evidence, that *N. amabilis* as recognized in recent ichthyological work comprises two separate species, both described by Girard (1856). The two species are chiefly distinguished based on differences in colour pattern, including arrangement of dark pigmentation on the dorsal surface of the head and dorsal midline, and the relationship between the dark lateral stripe along the side of the body and the lateral line. *Notropis amabilis* is distributed throughout the Gulf coast drainages traversing the Edwards Plateau of central Texas and the Rio Grande drainage of the southern United States and northern

Fig. 17. *Cyprinella lutrensis*, TCWC 14075.01, 51.0 mm SL, neotype of *C. luxiloides*: USA: Texas: San Antonio River.

Mexico. *Notropis megalops* is restricted entirely to the Rio Grande drainage, with a fragmented distribution throughout the Trans-Pecos region of Texas and Nuevo Leon (Mexico).

Comparative material: *Cyprinella lutrensis*: TCWC 14075.01, neotype of *C. luxiloides,* 51.0 mm SL; USA: Texas: Bexar Co.: San Antonio River, immediately downstream of Ashley Road, 29°19'57" N 98°27'47" W; 23 March 2004.

Notropis cf. *amabilis*: KU 3060, 1, 31.2 mm SL; Mexico: Chihuahua: Río San Pedro at confluence with Río Conchos, 28°20'40.3" N 105°24'26.9" W; 23 June 1953. – KU 5402, 19, 26.0–29.4 mm SL; Mexico: Chihuahua: Río San Pedro at confluence with Río Conchos, 28°20'40.3" N 105°24'26.9" W; 25 June 1959.

N. atherinoides: TCWC 385.01, 5, 49.1–57.5 mm SL; United States: Illinois: Whiteside Co.: Rock River 2.5 miles south of Como; 21 July 1964. – TCWC 3910.03, 5, 43.6–46.9 mm SL; United States: Texas: Wichita Co.: Red River 2 miles north west of Burkburnett on HW 240; 28 July 1984. – TCWC 14234.03, 12, 61.7–69.2 mm SL; United States: Oklahoma: Leflore Co.: Morris Creek at HW 59 crossing; 9 April 2000.

N. jemezanus: KU 8073, 20 (of 88), 29.4–40.1 mm SL; United States: New Mexico: Eddy Co.: Pecos River below dam at Lake McMillan; 23 April 1964. – KU 19432, 10, 45.2–54.8 mm SL; Mexico: Coahuila: overflow of Presa Don Martin; 12 March 1934. – TCWC 11045.01, 4, 25.4–45.8 mm SL; TCWC 11045.01, 1 (c&s), 37.0 mm SL; United States: Texas: Brewster Co.: Rio Grande 5.5 miles south east of confluence with Terlingua Creek; 10 June 1954. – OMNH 31272, 1, 33.9 mm SL; United States: Texas: Brewster Co.: Rio Grande at confluence with Tornillo Creek; 16 April 1960. – UMMZ 201506, 17, 17.1–43.7 mm SL; United States: Texas: Brewster Co.: Rio Grande halfway between Panther Rapids and San Francisco Canyon; 6 April 1977. – UMMZ 203178, 10, 54.4–68.5 mm SL; United States: New Mexico: Guadalupe Co.: Pecos River 6 miles below Santa Rosa; 13 May 1967. – UMMZ 212711, 36, 30.8–46.2 mm SL; United States: Texas: Webb Co.: Rio Grande at Laredo; 7 April 1939.

N. oxyrhynchus: TCWC 3908.02, 8, 44.2–49.8 mm SL; TCWC 3908.06, 3 (c&s), 39.0–47.0 mm SL; United States: Texas: Baylor Co.: Brazos River at FM 277 near Seymour; 28 July 1984. – TCWC 4060.09, 24, 25.4–43.3 mm SL; United States: Texas: Burleson Co.: Brazos River; 8 September 1972.

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Appendix 1. Species and specimens used for phylogenetic and genetic analyses, including museum voucher, code used in Figures 15–16, locality (drainage, river and lat/long) and Genbank accession numbers.

museum voucher	code	drainage	river	lat/long	Genbank number		
					cyt *b*	RAG1	S7
Agosia chrysogaster							
–	–	–	–	–	JX443014.1	JX443343.1	EU082743.1
Notropis amabilis							
TCWC 16329.07	AMAM1	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834439	KT834566	KT834600
TCWC 16329.07	AMAM2	San Antonio	Medina River	29°48'58"N / 99°15'33"W	–	KT834567	–
TCWC 16329.07	AMAM3	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834440	–	–
TCWC 16329.07	AMAM4	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834441	–	–
TCWC 16329.07	AMAM5	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834442	–	–
TCWC 16329.07	AMAM6	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834443	–	–
TCWC 16329.07	AMAM7	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834444	–	–
TCWC 16329.07	AMAM8	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834445	–	–
TCWC 16329.07	AMAM9	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834446	–	–
TCWC 16329.07	AMAM10	San Antonio	Medina River	29°48'58"N / 99°15'33"W	KT834447	–	–
TCWC 16322.10	AMAL1	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834448	KT834563	KT834601
TCWC 16322.10	AMAL2	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834449	KT834564	KT834602
TCWC 16322.10	AMAL3	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834450	–	–
TCWC 16322.10	AMAL4	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834451	–	–
TCWC 16322.10	AMAL5	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834452	KT834565	–
TCWC 16322.10	AMAL6	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834453	–	–
TCWC 16322.10	AMAL7	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834454	–	–
TCWC 16322.10	AMAL8	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834455	–	–
TCWC 16322.10	AMAL9	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834456	–	–
TCWC 16322.10	AMAL10	Colorado	Llano River	30°30'58"N / 99°48'20"W	KT834457	–	–
TCWC 16458.01	AMAC1	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834510	KT834555	–
TCWC 16458.01	AMAC2	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834511	–	–
TCWC 16458.01	AMAC3	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834512	KT834556	–
TCWC 16458.01	AMAC4	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834513	KT834557	–
TCWC 16458.01	AMAC5	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834514	KT834558	–
TCWC 16458.01	AMAC6	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834515	–	KT834632
TCWC 16458.01	AMAC7	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834516	KT834559	–
TCWC 16458.01	AMAC8	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834517	–	–
TCWC 16458.01	AMAC9	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834518	–	KT834633
TCWC 16458.01	AMAC10	Colorado	South Concho River	31°12'47"N / 100°30'02"W	KT834519	–	–
TCWC 15548.02	TEX1	Guadalupe	Johnson Creek	30°08'49"N / 99°20'18"W	KT834408	KT834571	KT834597
TCWC 16404.12	AMAB2	Guadalupe	Blanco River	29°59'08"N / 98°03'54"W	KT834478	–	KT834604
TCWC 16404.12	AMAB3	Guadalupe	Blanco River	29°59'08"N / 98°03'54"W	KT834479	–	–

museum voucher	code	drainage	river	lat/long	Genbank number		
					cyt *b*	RAG1	S7
Notropis amabilis (continued)							
TCWC 16404.12	AMAB4	Guadalupe	Blanco River	29°59'08"N / 98°03'54"W	KT834480	–	–
TCWC 16327.17	AMAF1	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834429	KT834560	KT834598
TCWC 16327.17	AMAF2	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834430	KT834561	KT834599
TCWC 16327.17	AMAF3	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834431	–	–
TCWC 16327.17	AMAF4	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834432	–	–
TCWC 16327.17	AMAF5	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834433	–	–
TCWC 16327.17	AMAF6	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834434	–	–
TCWC 16327.17	AMAF7	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834435	–	–
TCWC 16327.17	AMAF8	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834436	KT834562	–
TCWC 16327.17	AMAF9	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834437	–	–
TCWC 16327.17	AMAF10	Nueces	Frio River	29°36'18"N / 99°44'17"W	KT834438	–	–
TCWC 16326.12	AMAN1	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834419	KT834568	KT834603
TCWC 16326.12	AMAN2	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834420	–	–
TCWC 16326.12	AMAN3	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834421	–	–
TCWC 16326.12	AMAN4	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834422	–	–
TCWC 16326.12	AMAN5	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834423	–	–
TCWC 16326.12	AMAN6	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834424	–	–
TCWC 16326.12	AMAN7	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834425	–	–
TCWC 16326.12	AMAN8	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834426	KT834569	–
TCWC 16326.12	AMAN9	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834427	–	–
TCWC 16326.12	AMAN10	Nueces	Nueces River	29°23'53"N / 100°00'04"W	KT834428	–	–
TCWC 16325.12	AMAD1	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834458	KT834527	KT834582
TCWC 16325.12	AMAD2	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834459	KT834528	KT834583
TCWC 16325.12	AMAD3	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834460	–	–
TCWC 16325.12	AMAD4	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834461	KT834529	KT834584
TCWC 16325.12	AMAD5	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834462	KT834530	KT834585
TCWC 16325.12	AMAD6	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834463	–	KT834586
TCWC 16325.12	AMAD7	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834464	–	KT834587
TCWC 16325.12	AMAD8	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834465	–	–
TCWC 16325.12	AMAD9	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834466	–	–
TCWC 16325.12	AMAD10	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834467	–	–
TCWC 16457.01	AMAD16	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834468	–	KT834589
TCWC 16457.01	AMAD17	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834469	KT834531	KT834590
TCWC 16457.01	AMAD18	Rio Grande	Devils River	29°58'01"N / 101°08'57"W	KT834470	KT834532	KT834591
TCWC 16457.01	AMAD19	Rio Grande	Devils River	29°58'01"N / 101°8'57"W	KT834471	KT834533	KT834592
TCWC 16457.01	AMAD20	Rio Grande	Devils River	29°58'01"N / 101°8'57"W	KT834472	KT834534	KT834593
TCWC 16457.01	AMAD24	Rio Grande	Devils River	29°58'01"N / 101°8'57"W	KT834476	KT834538	KT834596

museum voucher	code	drainage	river	lat/long	Genbank number		
					cyt *b*	RAG1	S7
Notropis atherinoides							
TCWC uncat.	NAN1	Mississippi	Bear Creek	35°26'50" N / 89°57'44" W	KT834521	KT834573	KT834636
–	–	–	–	–	AF352273.1	HM224059.1	–
Notropis hudsonius							
KU 26947	HUD1	St. Lawrence	Mullett Lake	45°33'36" N / 84°31'35" W	KT834523	KT834574	KT834637
Notropis jemezanus							
MSB 100359	JEME1	Rio Grande	Pecos River	–	–	KT834572	–
MSB 100359	JEME2	Rio Grande	Pecos River	–	KT834520	–	KT834634
–	–	Rio Grande	Pecos River	–	AF352277.1	–	–
Notropis megalops							
TCWC 16455.06	AMAS1	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834481	KT834539	KT834605
TCWC 16455.06	AMAS2	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834482	KT834540	KT834606
TCWC 16455.06	AMAS3	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834483	KT834541	KT834607
TCWC 16455.06	AMAS4	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834484	–	KT834608
TCWC 16455.06	AMAS5	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834485	KT834542	KT834609
TCWC 16455.06	AMAS6	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834486	KT834543	KT834610
TCWC 16455.06	AMAS7	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834487	KT834544	KT834611
TCWC 16455.06	AMAS8	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834488	KT834545	KT834612
TCWC 16455.06	AMAS9	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834489	KT834546	KT834613
TCWC 16455.06	AMAS10	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834490	KT834547	KT834614
TCWC 16455.06	AMAS11	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834491	KT834548	KT834615
TCWC 16455.06	AMAS12	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834492	–	KT834616
TCWC 16455.06	AMAS13	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834493	–	KT834617
TCWC 16455.06	AMAS14	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834494	–	KT834618
TCWC 16455.06	AMAS15	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834495	–	KT834619
TCWC 16455.06	AMAS16	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834496	–	KT834620
TCWC 16455.06	AMAS17	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834497	–	–
TCWC 16455.06	AMAS18	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834498	–	KT834621
TCWC 16455.06	AMAS19	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	–	–	–
TCWC 16455.06	AMAS20	Rio Grande	San Felipe Creek	29°21'15" N / 100°53'45" W	KT834499	–	KT834622
TCWC 15558.02	AMA1	Rio Grande	Devils River	29°58'01" N / 101°08'57" W	KT834477	KT834570	KT834588
TCWC 16457.02	AMAD21	Rio Grande	Devils River	29°58'01" N / 101°08'57" W	KT834473	KT834535	–
TCWC 16457.02	AMAD22	Rio Grande	Devils River	29°58'01" N / 101°08'57" W	KT834474	KT834536	KT834594
TCWC 16457.02	AMAD23	Rio Grande	Devils River	29°58'01" N / 101°08'57" W	KT834475	KT834537	KT834595
TCWC 16323.14	AMAI1	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834409	KT834524	KT834575
TCWC 16323.14	AMAI2	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834410	KT834525	KT834576
TCWC 16323.14	AMAI3	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834411	–	KT834577
TCWC 16323.14	AMAI4	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834412	–	–
TCWC 16323.14	AMAI5	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834413	KT834526	KT834578

museum voucher	code	drainage	river	lat/long	Genbank number		
					cyt *b*	RAG1	S7
Notropis megalops (continued)							
TCWC 16323.14	AMAI6	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834414	–	–
TCWC 16323.14	AMAI7	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834415	–	KT834579
TCWC 16323.14	AMAI8	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834416	–	KT834580
TCWC 16323.14	AMAI9	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834417	–	KT834581
TCWC 16323.14	AMAI10	Rio Grande	Independence Creek	30°27'36" N / 101°49'30" W	KT834418	–	–
TCWC 16456.11	AMAP1	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834500	KT834549	KT834623
TCWC 16456.11	AMAP2	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834501	KT834550	KT834624
TCWC 16456.11	AMAP3	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834502	KT834551	KT834625
TCWC 16456.11	AMAP4	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834503	KT834552	–
TCWC 16456.11	AMAP5	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834504	KT834553	KT834626
TCWC 16456.11	AMAP6	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834505	KT834554	KT834627
TCWC 16456.11	AMAP7	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834506	–	KT834628
TCWC 16456.11	AMAP8	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834507	–	KT834629
TCWC 16456.11	AMAP9	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834508	–	KT834630
TCWC 16456.11	AMAP10	Rio Grande	Pecos River	30°07'41" N / 101°34'23" W	KT834509	–	KT834631
Notropis percobromus							
TCWC uncat.	NPB1	Mississippi	Vermilion River	40°05'06" N / 87°35'37" W	KT834522	–	KT834635
Notropis stilbius							
–	–	–	–	–	AF352286.1	GU136338.1	GU134241.1
Pimephales vigilax							
–	–	–	–	–	GQ184534.1	GU136356.1	GU134261.1