Reconciling Genetic Lineages with Species in Western Atlantic *Coryphopterus* (Teleostei: Gobiidae)

Carole C. Baldwin, Lee A. Weigt, David G. Smith, and Julie H. Mounts

ABSTRACT. Species identification of western Atlantic *Coryphopterus* can be problematic because some of the species are morphologically similar, there is confusing morphological variation within some species, no taxonomic key includes all currently recognized species, and the validity of some species is questionable. The most recently published keys do not include *Coryphopterus tortugae* or *C. venezuelae*, the validity of which as distinct from *C. glaucofraenum* has been questioned. Neighbor-joining trees derived from mitochondrial cytochrome *c* oxidase I (COI) sequences (DNA barcoding) were used to determine the number of genetically distinct lineages of *Coryphopterus* from collections made off Belize, Curacao, and Florida. Additional specimens for genetic and morphological analysis were obtained from Panama, Venezuela, and the Bahamas. Subsequent comparative analysis of preserved voucher specimens from which DNA was extracted and digital color photographs of those specimens taken before preservation yielded, in most cases, sufficient morphological information to separate the genetic lineages. Species identification of the lineages was then determined based on review of original and subsequent descriptions of *Coryphopterus* species and examination of museum specimens, including some type material. Many museum specimens are misidentified. Twelve species of *Coryphopterus* are herein recognized in the western Atlantic and Caribbean: *C. alloides*, *C. dicrus*, *C. eidolon*, *C. glaucofraenum*, *C. hyalinus*, *C. kuna*, *C. lipernes*, *C. personatus*, *C. punctipectophorus*, *C. thrix*, *C. tortugae*, and *C. venezuelae*. *Coryphopterus bol* Victor, 2008 is a synonym of *C. venezuelae* (Cervigón, 1966). Although genetically distinct, *C. glaucofraenum* and some specimens of *C. venezuelae* are extremely similar and cannot be separated on the basis of morphology 100% of the time. Comments on the identification of each *Coryphopterus* species and a revised key to western Atlantic species are provided.

INTRODUCTION

To provide specific identifications of larvae of Caribbean reef fishes at Carrie Bow Cay, Belize, a small coral-fringed island on the Belizean Barrier Reef (16°48.5′N, 88°05′W), we have been matching larvae to adults through DNA barcoding (mitochondrial cytochrome c oxidase I [COI] sequences). In addition to greatly increasing our success rate of identifying larvae, DNA barcoding is also providing a method of checking existing species-level classifications by revealing the numbers of distinct genetic lineages within genera.

Carole C. Baldwin, Lee A. Weigt, David G. Smith, and Julie H. Mounts, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013–7012, USA. Corresponding author: C. Baldwin (baldwinc@si.edu). *Received 13 May 2008; accepted 20 April 2009.*

Attempts to identify Belizean *Coryphopterus* species using the most recently published keys (Böhlke and Robins, 1960, 1962; Böhlke and Chaplin, 1968; Murdy, 2002) proved problematic for certain species. None of those keys includes *C. tortugae* (Jordan) or *C. venezuelae* Cervigón, presumably because the validity of both species as distinct from *C. glaucofraenum* Gill has been questioned (e.g., Böhlke and Robins, 1960; Cervigón, 1966; Thacker and Cole, 2002). Longley and Hildebrand (1941) and Böhlke and Robins (1960) considered *C. tortugae* (Jordan; type locality, Dry Tortugas, Florida) a synonym of *C. glaucofraenum* Gill. Garzón-Ferreira and Acero (1990) redescribed *C. tortugae* as distinct based on new collections from the Colombian Caribbean. Thacker and Cole (2002) acknowledged the latter work but did not recognize *C. tortugae* in their phylogenetic analysis of *Coryphopterus* species. Victor (2008) recognized *C. tortugae* as distinct from *C. glaucofraenum* and identified what he considered a cryptic new species within Garzón-Ferreira and Acero's (1990) *C. tortugae*, which he named *Coryphopterus bol.* Cervigón (1994) elevated *C. venezuelae* from a subspecies of *C. glaucofraenum* to a distinct species, but it was not included in Murdy's (2002) key or Thacker and Cole's (2002) and Victor's (2008) molecular phylogenies of *Coryphopterus* species.

Another problem with identification of western Caribbean *Coryphopterus* is that stated distributions of many species are conflicting, and some do not include the western Caribbean. Greenfield and Johnson (1999) identified nine species of *Coryphopterus* from Belize (all of the 12 recognized herein except for *C. venezuelae*, *C. punctipectophorus*, and the recently described *C. kuna* (Victor, 2007)). Murdy (2002) listed only *C. alloides*, *C. dicrus*, *C. glaucofraenum*, *C. hyalinus*, *C. lipernes*, and *C. personatus* as having ranges that include Central America, western Caribbean, or Caribbean. A search for reef-associated species in Belize in FishBase (www.fishbase.org) returned only *C. alloides*, *C. eidolon*, *C. glaucofraenum*, and *C. personatus*.

The purposes of this paper are to assess the number of valid *Coryphopterus* species known from the western Atlantic and to provide comments on the identification of, and a revised key to, those species based on results of DNA barcoding, subsequent examination of voucher specimens and color photographs of them, examination of museum specimens, and reference to original and other descriptions of the species. A neotype for *C. glaucofraenum* is designated because the location of Gill's (1863) holotype is unknown.

METHODS

Depending on the locality, fish specimens were collected using the fish anesthetic quinaldine sulfate or rotenone. Specimens were measured to the nearest 0.5 mm, photographed with a Fujifilm FinePix 3 digital camera to record color patterns, sampled for genetic analysis, and then preserved as vouchers. Tissue sampling for molecular work involved removing a muscle biopsy, eye, or caudal body portion (depending on size) and storage in saturated salt buffer (Seutin et al., 1990). Genomic DNA was extracted from up to approximately 20 mg minced preserved tissue via an automated phenol:chloroform extraction on the Autogenprep965 (Autogen, Holliston, MA) using the mouse tail tissue protocol with a final elution volume of 50 μL. For polymerase chain reaction (PCR), 1 μL of this genomic DNA is used in a 10 μL reaction with 0.5 U Bioline (BioLine USA, Boston, MA) Taq polymerase, 0.4 μL 50 mM $MgCl_2$, 1 μL 10× buffer, 0.5 μL 10 mM deoxyribonucleotide triphosphate (dNTP), and 0.3 μL 10 μM each primer FISH-BCL (5′-TCAACYAATCAYAAAGATATYGGCAC) and FISH-BCH (5′-TAAACTTCAGGGTGACCAAAAAATCA). The thermal cycler program for PCR was 1 cycle of 5 min at 95°C; 35 cycles of 30 s at 95°C, 30 s at 52°C, and 45 s at 72°C; 1 cycle of 5 min at 72°C; and a hold at 10°C. The PCR products were purified with Exosap-IT (USB, Cleveland, OH) using 2 μL 0.2× enzyme and incubated for 30 min at 37°C. The reaction was then inactivated for 20 min at 80°C. Sequencing reactions were performed using 1 μL of this purified PCR product in a 10 μL reaction containing 0.5 μL primer, 1.75 μL BigDye buffer, and 0.5 μL BigDye (ABI, Foster City, CA) and run in the thermal cycler for 30 cycles of 30 s at 95°C, 30 s at 50°C, 4 min at 60°C, and then held at 10°C. These sequencing reactions were purified using Millipore Sephadex plates (MAHVN-4550; Millipore, Billerica, MA) per manufacturer's instructions and stored dry until analyzed. Sequencing reactions were analyzed on an ABI 3730XL automated DNA sequencer, and sequence trace files were exported into Sequencher 4.7 (GeneCodes, Ann Arbor, MI). Using the Sequencher program, ends were trimmed from the raw sequences until the first and last 10 bases contained fewer than 5 base calls with a confidence score (phred score) lower than 30. After trimming, forward and reverse sequences for each specimen were assembled, each assembled contig was examined and edited by hand, and each sequence was checked for stop codons. Finally the consensus sequence from each contig was aligned and exported in a nexus format. Neighbor-joining trees (Saitou and Nei, 1987) and

distance matrices were generated using Paup*4.1 (Swofford, 2002) on an analysis of Kimura 2-parameter (K2P) distances (Kimura, 1980).

MATERIAL

The *Coryphopterus* material examined is listed in the Appendix (Table A.1). This table includes the voucher specimens represented in the neighbor-joining tree (Figure 1), as well as non-voucher specimens collected as part of this or other projects. Most specimens examined genetically for this chapter are juveniles or adults, except those of *C. kuna*; that species is represented in our samples only by larvae. For most specimens analyzed genetically, a digital color photograph of the specimen taken before dissection and preservation is housed at the Smithsonian Institution. Cytochrome *c* oxidase I (COI) sequences for specimens analyzed genetically are deposited in GenBank (accession numbers GQ367306–GQ367475). Genetic information for several specimens collected in the Bahamas was not available in time for inclusion in the neighbor-joining tree, but identifications of those specimens based on that information are discussed in the text.

RESULTS

Twelve distinct genetic lineages of *Coryphopterus* are present in our material (see Figure 1). One of those lineages, a single specimen identified as *C. alloides* from Curacao is under additional investigation and is not discussed further here. Tissue samples of *C. punctipectophorus* were not available for genetic analysis. The other lineages, from top to bottom in Figure 1, are *C. lipernes*, *C. hyalinus*, *C. personatus*, *C. tortugae*, *C. glaucofraenum*, *C. venezuelae*, *C. dicrus*, *C. thrix*, *C. eidolon*, *C. alloides*, and *C. kuna*. Comments on the identification of each lineage, as well as *C. punctipectophorus*, are provided below. The COI sequence of *Coryphopterus bol* Victor, 2008 (PR SIO0869, fig. 1 [SIO = Scripps Institution of Oceanography]) is part of the *C. venezuelae clade*, and the synonymy of that species is discussed below. Intra- and interspecific differences in percent sequence divergence for COI for all species are provided in Table 1. We have not plotted distribution maps of *Coryphopterus* species because our samples are from a limited number of locations, and historical confusion about the identification of some species precluded our relying on geographic information based on museum catalogues. Based on extensive recent collecting throughout the Caribbean, Ross Robertson (Smithsonian Tropical Research Institute, personal communication, 8 June 2009) and James Van Tassell are providing distribution maps of *Coryphopterus* species in their *Shorefishes of the Greater Caribbean* CD, expected to be released in 2009.

Coryphopterus lipernes Böhlke and Robins, 1962

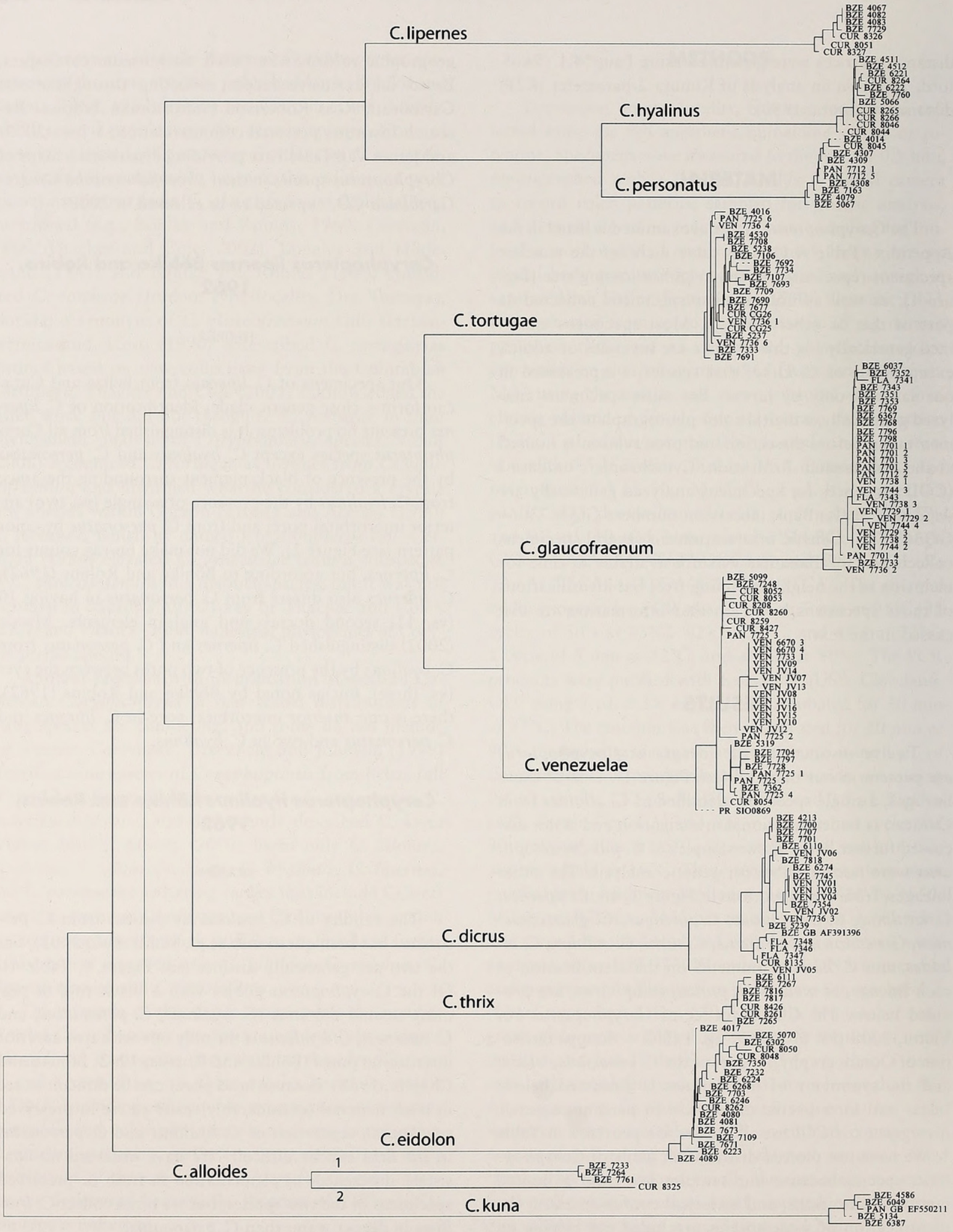
FIGURE 2

Our specimens of *C. lipernes* from Belize and Curacao form a close genetic clade. Identification of *C. lipernes* presents no problems: It is distinguished from all *Coryphopterus* species except *C. hyalinus* and *C. personatus* by the presence of black pigment surrounding the anus; from *C. hyalinus* by the presence of a single (vs. two) anterior interorbital pore; and from *C. personatus* by color pattern (see Figure 2). We did not make fin-ray counts for *C. lipernes*, but according to Böhlke and Robins (1962), *C. lipernes* also differs from *C. personatus* in having 10 (vs. 11) second dorsal- and anal-fin elements. Murdy (2002) distinguished *C. lipernes* and *C. personatus* from *C. hyalinus* by the presence of two pores between the eyes (vs. three), but as noted by Böhlke and Robins (1962), there is one *anterior* interorbital pore in *C. lipernes* and *C. personatus* and two in *C. hyalinus*.

Coryphopterus hyalinus Böhlke and Robins, 1962

FIGURE 2

The validity of *C. hyalinus* as distinct from *C. personatus* has been questioned (e.g., Smith et al., 2003), but the two are genetically distinct (see Figure 1, Table 1). Of the *Coryphopterus* gobies with a black ring of pigment around the anus (*C. hyalinus*, *C. personatus*, and *C. lipernes*), *C. hyalinus* is the only one with two anterior interorbital pores (Böhlke and Robins, 1962; Böhlke and Chaplin, 1968). Because head pores can be difficult to see in fresh material (considerably easier to see in preserved specimens), separation of *C. hyalinus* and *C. personatus* in the field can be difficult. We have observed no consistent differences in pigmentation in fresh or preserved specimens of the two species, but we often collect *C. hyalinus* in deeper water than *C. personatus*.


C. lipernes
C. hyalinus
C. personatus
C. tortugae
C. glaucofraenum
C. venezuelae
C. dicrus
C. thrix
C. eidolon
C. alloides
C. kuna
1
2
BZE 4067
BZE 4082
BZE 4083
BZE 7729
CUR 8326
CUR 8051
CUR 8327
BZE 4511
BZE 4512
BZE 6221
CUR 8264
BZE 6222
BZE 7760
BZE 5066
CUR 8265
CUR 8266
CUR 8046
CUR 8044
BZE 4014
CUR 8045
BZE 4307
BZE 4309
PAN 7712 1
PAN 7712 5
BZE 4308
BZE 7163
BZE 4079
BZE 5067
BZE 4016
PAN 7725 6
VEN 7736 4
BZE 4530
BZE 7708
BZE 5238
BZE 7106
BZE 7692
BZE 7734
BZE 7107
BZE 7693
BZE 7709
BZE 7690
BZE 7677
CUR CG26
VEN 7736 1
CUR CG25
BZE 5237
VEN 7736 6
BZE 7333
BZE 7691
BZE 6037
BZE 7352
FLA 7341
BZE 7343
BZE 7351
BZE 7353
BZE 7769
BZE 6367
BZE 7768
BZE 7796
BZE 7798
PAN 7701 1
PAN 7701 2
PAN 7701 3
PAN 7701 5
PAN 7712 2
VEN 7738 1
VEN 7744 3
FLA 7343
VEN 7738 3
VEN 7729 1
VEN 7729 2
VEN 7744 4
VEN 7729 3
VEN 7738 2
VEN 7744 2
PAN 7701 4
BZE 7733
VEN 7736 2
BZE 5099
BZE 7248
CUR 8052
CUR 8053
CUR 8208
CUR 8260
CUR 8259
CUR 8427
PAN 7725 3
VEN 6670 3
VEN 6670 4
VEN 7733 1
VEN JV09
VEN JV14
VEN JV07
VEN JV13
VEN JV08
VEN JV11
VEN JV16
VEN JV15
VEN JV10
VEN JV12
PAN 7725 2
BZE 5319
BZE 7704
BZE 7797
BZE 7728
PAN 7725 1
PAN 7725 5
BZE 7362
PAN 7725 4
CUR 8054
PR SIO0869
BZE 4213
BZE 7700
BZE 7707
BZE 7701
BZE 6110
VEN JV06
BZE 7818
BZE 6274
BZE 7745
VEN JV01
VEN JV03
VEN JV04
BZE 7354
VEN JV02
VEN 7736 3
BZE 5239
BZE GB AF391396
FLA 7348
FLA 7346
FLA 7347
CUR 8135
VEN JV05
BZE 6111
BZE 7267
BZE 7816
BZE 7817
CUR 8426
CUR 8261
BZE 7265
BZE 4017
BZE 5070
BZE 6302
CUR 8050
CUR 8048
BZE 7350
BZE 7232
BZE 6224
BZE 6268
BZE 7703
BZE 6246
CUR 8262
BZE 4080
BZE 4081
BZE 7673
BZE 7109
BZE 7671
BZE 6223
BZE 4089
BZE 7233
BZE 7264
BZE 7761
CUR 8325
BZE 4586
BZE 6049
PAN GB EF550211
BZE 5134
BZE 6387
0.005 substitutions/site

Coryphopterus personatus (Jordan and Thompson, 1905)

FIGURE 2

Identification of *C. personatus* also presents no problems using published keys. It can be distinguished from *C. hyalinus* by the presence of a single interorbital pore and from *C. lipernes* by pigment pattern (see Figure 2). According to Böhlke and Robins (1962), *C. personatus* also can be separated from *C. lipernes* by having 11 (vs. 10) total elements in the second dorsal and anal fins.

Coryphopterus tortugae (Jordan, 1904)

FIGURE 3

Longley and Hildebrand (1941) and Böhlke and Robins (1960) considered *C. tortugae* (Jordan: type locality, Dry Tortugas, Florida) to be a synonym of *C. glaucofraenum* Gill. Garzón-Ferreira and Acero (1990) redescribed *C. tortugae* as distinct based on new collections from the Colombian Caribbean. Victor (2008) concurred with Garzón-Ferreira and Acero's (1990) recognition of *C. tortugae* but noted that their Santa Marta specimens constitute a distinct species, which he described as *C. bol*. As noted below (see "Synonymy of *Coryphopterus bol*"), *C. bol* appears to be a synonym of *C. venezuelae*.

We had initially identified all specimens of the *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* clades as *C. glaucofraenum* using published keys (Böhlke and Robins, 1960; Böhlke and Chaplin, 1968; Murdy, 2002). However, those specimens separate into three well-defined lineages based on COI sequences. Specimens in one of those lineages are usually paler than those of the other two and almost always have a central bar of basicaudal pigment (vs. usually two spots or a dumbbell- or C-shaped marking), characters described by Garzón-Ferreira and Acero (1990) as diagnostic for *C. tortugae*. Böhlke and Robins (1960), who considered *C. tortugae* to be a pallid form of *C. glaucofraenum*, noted that the pigment markings along the side of the body are round (upper row) or vertically elongate (lower row) versus X-shaped as in *C. glaucofraenum*, usually a consistent feature in our specimens of *C. tortugae*. The pigment spots in the lower row of markings along the side of the body in *C. tortugae* are usually vertically elongate (crescents or some part of an X), but they are rarely distinct X-shaped markings. If some of the anterior markings do resemble X's (Figure 3D), the height of each X is considerably smaller than the height of the X's in *C. glaucofraenum* and, when present, in *C. venezuelae* (half or less of eye diameter in *C. tortugae*, approximately three-quarters of or equal to eye diameter in the other two species). The pigment spots in the lower row also are not rounded, as they are in pale specimens of *C. venezuelae*.

We have not found the basicaudal pigment to be a reliable character for separating *C. tortugae* from *C. glaucofraenum* and *C. venezuelae*, as all three species may have a central bar of pigment; however, *C. tortugae* does not have two distinct spots in any of our material, so if that feature is present in a specimen, it is not *C. tortugae*. *Coryphopterus tortugae* shares with *C. glaucofraenum* and *C. venezuelae* the presence of a distinct dark blotch or triangle behind the eye above the opercle and with *C. glaucofraenum* the absence of a pigment spot on the lower portion of the pectoral-fin base. Garzón-Ferreira and Acero's (1990) redescription of *C. tortugae* did not mention the absence of this spot, presumably because the Santa Marta specimens included in their description do have the spot and appear to be *C. venezuelae* (see "Synonymy of *Coryphopterus bol*," below). Our investigations indicate that the absence of this pigment spot on the pectoral-fin base, along with the presence of vertically elongate versus round pigment spots in the lower row of markings on the body, is significant in separating *C. tortugae* from pale specimens of *C. venezuelae*. Examination of photographs of the holotype of *Ctenogobius tortugae* (SU 8363) confirms that there is no pigment on the lower portion of the pectoral-fin base.

Coryphopterus tortugae is most easily separated from all other *Coryphopterus* by the following combination of characters: a dark blotch or triangle of pigment above the opercle is present; large X-shape markings on the side of the body and a spot on the lower pectoral-fin base are absent; at least some of the pigment markings in the lower row along the side of the body are vertically elongate or crescent shaped; and the overall coloring is pale.

Coryphopterus glaucofraenum Gill, 1864

FIGURE 4

The location of the single type specimen upon which Gill described *C. glaucofraenum* is unknown (Eschmeyer, 2008). Böhlke and Robins (1960:108–109) described

FIGURE 1. (*facing page*) Neighbor-joining tree derived from cytochrome *c* oxidase I sequences showing genetically distinct lineages of western Atlantic *Coryphopterus*.

TABLE 1. Average (and range) Kimura two-parameter distance summary for *Coryphopterus* species based on cytochrome *c* oxidase I (COI) sequences of individuals represented in the neighbor-joining tree in Figure 1. Intraspecific averages are shown in bold; n/a = data not available.

Coryphopterus sp.	*lipernes* (*n* = 7)	*hyalinus* (*n* = 11)	*personatus* (*n* = 10)	*tortugae* (*n* = 21)	*glaucofraenum* (*n* = 29)	*venezuelae* (*n* = 33)	*dicrus* (*n* = 22)	*thrix* (*n* = 7)	*eidolon* (*n* = 19)	*alloides* 1 (*n* = 3)	*alloides* 2 (*n* = 1)	*kuna* (*n* = 5)
lipernes	**0.13%** (0.00–0.35)	–	–	–	–	–	–	–	–	–	–	–
hyalinus	14.88% (14.21–15.40)	**0.06%** (0.00–0.31)	–	–	–	–	–	–	–	–	–	–
personatus	15.66% (15.10–16.03)	7.14% (6.79–7.65)	**0.14%** (0.00–0.46)	–	–	–	–	–	–	–	–	–
tortugae	19.60% (18.65–20.23)	21.14% (20.64–21.82)	20.08% (19.46–21.02)	**0.20%** (0.00–0.61)	–	–	–	–	–	–	–	–
glaucofraenum	20.71% (19.49–21.20)	21.68% (20.61–22.44)	21.50% (20.48–22.30)	12.07% (11.07–12.99)	**0.19%** (0.00–0.92)	–	–	–	–	–	–	–
venezuelae	21.37% (19.27–22.13)	20.86% (19.59–21.69)	20.12% (18.58–21.18)	9.84% (8.10–10.77)	9.51% (8.59–10.21)	**0.53%** (0.00–1.24)	–	–	–	–	–	–
dicrus	21.72% (20.10–22.56)	19.68% (18.61–20.37)	19.03% (18.30–19.94)	17.53% (16.59–18.07)	20.65% (19.82–21.32)	18.28% (16.46–19.00)	**0.61%** (0.00–2.82)	–	–	–	–	–
thrix	21.86% (20.85–22.69)	21.10% (20.11–22.44)	19.70% (19.19–20.48)	19.00% (18.43–19.63)	21.03% (20.30–21.54)	19.30% (17.61–20.12)	21.30% (20.74-21.84)	**0.11%** (0.00–0.48)	–	–	–	–
eidolon	25.16% (24.45–26.19)	19.19% (18.19–20.11)	17.92% (17.12–18.82)	19.74% (18.34–21.42)	23.17% (21.98–25.04)	18.72% (16.75–20.36)	19.39% (18.69–20.87)	19.54% (18.96–20.41)	**0.24%** (0.00–0.99)	–	–	–
alloides 1	22.13% (21.53–22.53)	17.90% (17.09–18.64)	18.16% (17.69–18.93)	19.44% (18.79–20.14)	21.69% (20.98–22.48)	18.62% (17.67–19.70)	18.15% (17.52–19.03)	20.39% (19.91–21.18)	18.06% (17.28–19.08)	**0.21%** (0.16–0.31)	–	–
alloides 2	21.15 (21.02–21.68)	17.75% (17.62–17.96)	19.27% (19.04–19.94)	21.73% (21.38–22.18)	21.30% (21.04–21.81)	19.68% (18.58–20.23)	17.11% (16.70–17.80)	19.16% (19.10–19.38)	19.34% (18.82–19.90)	9.68% (9.48–9.88)	**n/a** n/a	–
kuna	26.41 (25.59–27.00)	23.22% (22.62–23.65)	25.70% (24.86–26.37)	25.51% (24.58–26.27)	27.87% (26.79–28.53)	25.78% (24.48–26.64)	24.91% (23.36–25.57)	25.63% (24.96–26.27)	25.54% (24.61–26.20)	23.30% (22.77–23.65)	23.97% (23.59–24.30)	**0.57%** (0.15–1.24)

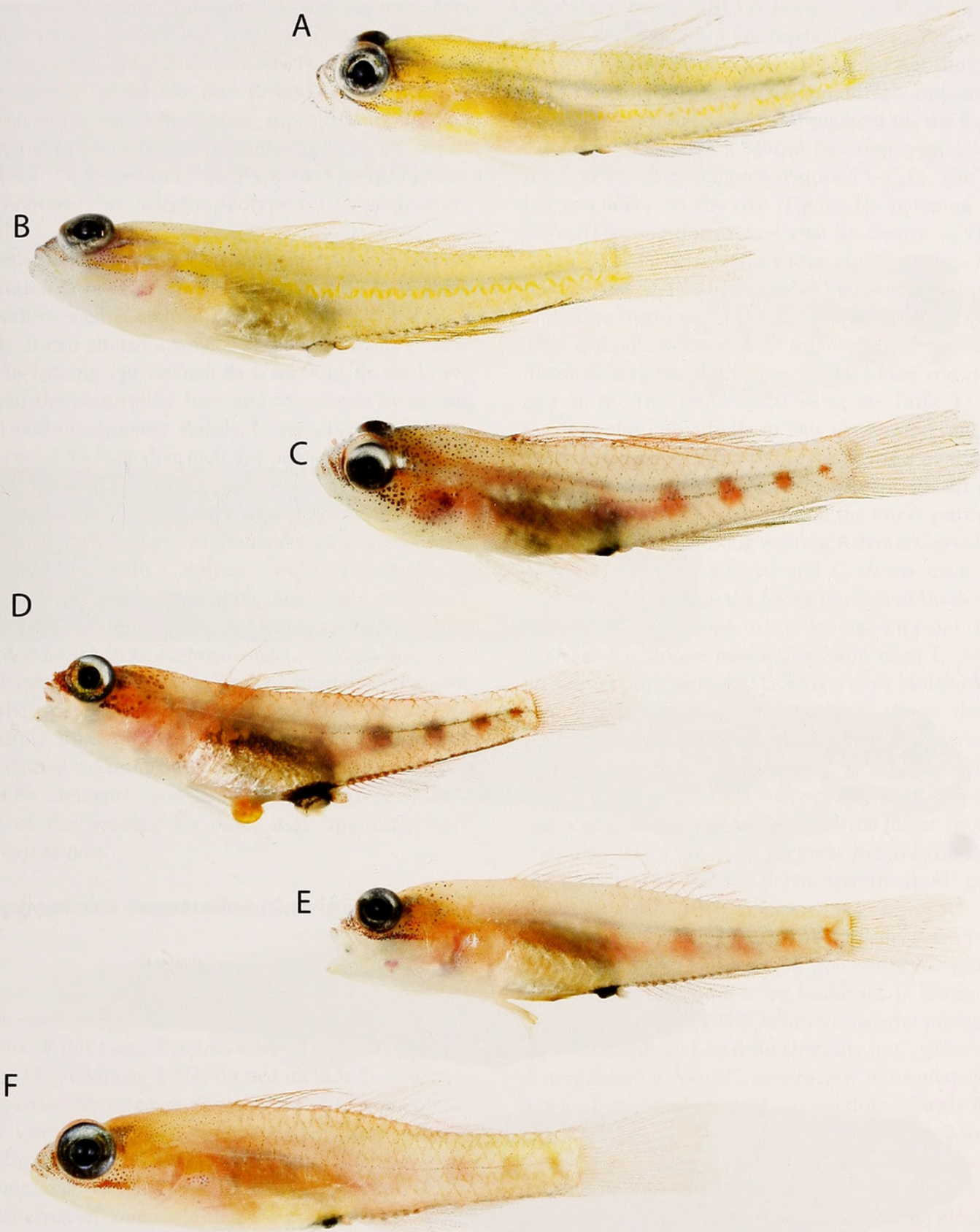


FIGURE 2. *Coryphopterus lipernes*: A, Curacao, 20 mm SL, DNA 8326, USNM 394896; B, Curacao, 21 mm SL, DNA 8051, USNM 394895. *Coryphopterus hyalinus*: C, Curacao, 20 mm SL, DNA 8044, USNM 394890; D, Curacao, 17 mm SL, DNA 8265, USNM 294889. *Coryphopterus personatus*: E, Curacao, 21 mm SL, DNA 8045, USNM 294897; F, Belize, 15 mm SL, DNA 7163, USNM 394742.

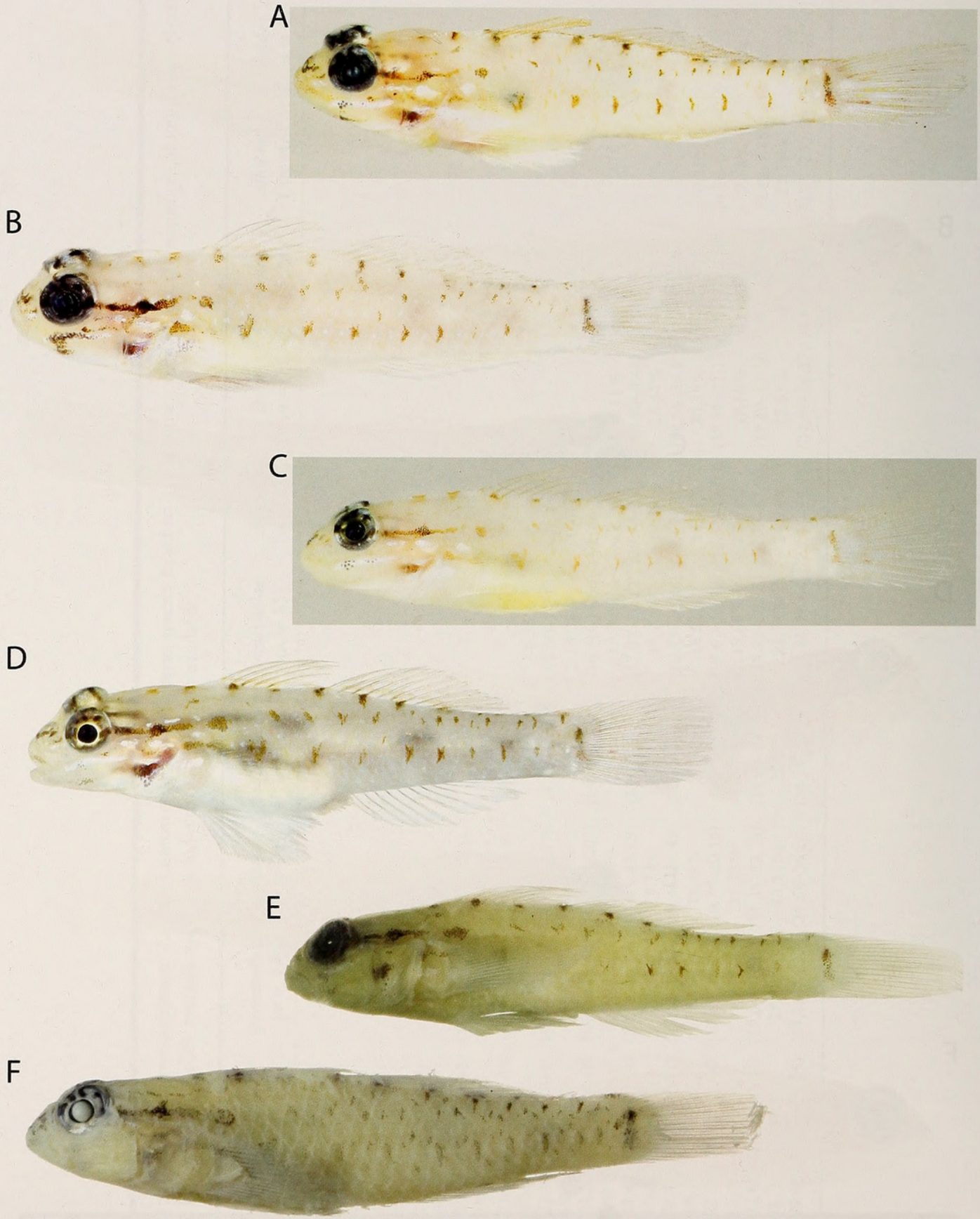


FIGURE 3. *Coryphopterus tortugae*: A, Belize, 25 mm SL, DNA 7333, USNM 394744; B, Belize, 34 mm SL, DNA 5237, USNM 394743; C, Belize, 36 mm SL, DNA 7107, USNM 394733; D, Belize, 40 mm SL, DNA 4530, USNM 394730; E, Belize, 40 mm SL, DNA 4530, USNM 394730, preserved; F, Venezuela, 37 mm SL, DNA 7736 4, AMNH 247340, alcohol preserved.

two forms of *C. glaucofraenum*: "[D]ark inshore form (typical *glaucofraenum*)" and"[P]allid white-sand form." Specimens in our genetic clade identified as *C. glaucofraenum* match the Böhlke and Robins (1960) "typical *glaucofraenum*," an identification supported by the fact that the pallid form is now recognized as *C. tortugae*. Below (see "Designation of Neotype for *Coryphopterus glaucofraenum*") we select a neotype for *C. glaucofraenum* Gill.

In our material, adult *C. glaucofraenum* can always be separated from *C. tortugae* by having at least some large, well-formed X-shaped markings along the side of the body. It can almost always be separated from *C. venezuelae* by lacking a prominent dark marking on the lower portion of the pectoral-fin base and sometimes by having 10 total anal-fin elements. Rarely, *C. glaucofraenum* has a dark pectoral-fin base that includes pigment on the lower portion (Figure 4G), and *C. venezuelae* may have 9–11 anal-fin elements, 10 being the typical count in our material (Table 2). *Coryphopterus glaucofraenum* usually can be separated from both *C. tortugae* and *C. venezuelae* by the shape of the pigment marking above the opercle: a two-peaked blotch in *C. glaucofraenum*, and a triangular or rounded blotch in *C. tortugae* and *C. venezuelae*.

If a specimen has a two-peaked blotch of pigment above the opercle, has at least some large (height approximately three-quarters of or equal to diameter of eye) X-shaped markings along the side of the body, has 10 anal-fin elements, and lacks pigment on the lower portion of the pectoral-fin base, it is unquestionably *C. glaucofraenum*.

Coryphopterus venezuelae (Cervigón, 1966)

FIGURE 5

The most recent keys to western Atlantic *Coryphopterus* (Böhlke and Robins, 1960, 1962; Böhlke and Chaplin, 1968; Murdy 2002) do not include *C. venezuelae*, originally described as a subspecies of *C. glaucofraenum* by Cervigón (1966), but recognized as a separate species by Cervigón (1994) and known at the time only from Venezuela. In the *Coryphopterus* material from the northeast coast of Venezuela that we examined are specimens that are clearly *C. venezuelae* based on Cervigón's (1966, 1994) descriptions: most notably the presence of 11 second dorsal- and anal-fin elements, a dark blotch of pigment on the lower portion of the pectoral-fin base, and two dark spots on the base of the caudal fin (e.g., Figure 5D herein). However, those Venezuelan specimens are part of a clade based on COI analysis (see Figure 1) that includes specimens from Venezuela, Curacao, Panama, Belize, Puerto Rico, and the Bahamas (the last not shown on the tree) that usually have 10 second dorsal- and anal-fin elements and various patterns of pigment on the base of the caudal fin, including a central bar, two spots joined by a bar, and a C-shaped blotch (Figure 5A–C,E). The Venezuelan specimens on the tree (Figure 1), including two that have 10 second dorsal- and anal-fin elements (VEN 7733 1 and VEN JV12), cluster within the *C. venezuelae* clade, but the genetic distance between the Venezuelan specimens and other members of the clade is only 0.41% to 0.85%. This distance is extremely small relative to the genetic distance between the *C. venezuelae* clade and other species on the tree (9.51%–20.86%; see Table 1), suggesting that the individuals in this clade represent a single species. Corroborating the identification of the clade as Cervigón's *C. venezuelae* is the presence in all individuals in the clade of a dark spot on the lower portion of the pectoral-fin base. Among western Atlantic *Coryphopterus*, only *C. punctipectophorus* and *C. dicrus* have a prominent pigment spot on the lower portion of the pectoral-fin base: *C. punctipectophorus* is not known from the Caribbean, and it differs morphologically from *C. venezuelae* in, among other features, lacking a dark blotch of pigment behind the eye above the opercle; in *C. dicrus*, there is also a prominent spot of equal size on the dorsal portion of the pectoral base that is lacking in *C. venezuelae* (which may have a slash of pigment but never a well-defined dorsal spot equal in size and intensity to the lower spot); *C. dicrus* also lacks the dark pigment behind the eye above the opercle and lacks a pelvic frenum (both present in *C. venezuelae*).

Our data thus suggest that *C. venezuelae* is a much more widespread species than previously recognized, and fin-ray counts alone are not sufficient in diagnosing the species. Cervigón (1994) believed that the presence of 10 second dorsal- and anal-fin elements in *C. glaucofraenum* distinguished it from *C. venezuelae*. In his material of the latter, all specimens had 11 second dorsal-fin elements and most had 11 anal-fin elements (two had 10). Most of our specimens of *C. glaucofraenum* have 10 second dorsal- and anal-fin elements, but two specimens have 11 second dorsal-fin elements, and two have 9 anal-fin elements (see Table 2). Both 10 and 11 second dorsal- and anal-fin elements are common in specimens in our *C. venezuelae* clade (Table 3), although we found 11 in both fins only in some of our material from Venezuela. It is significant that one of the *C. venezuelae* specimens from Venezuela that has 10 elements in both fins was caught in the same sample as

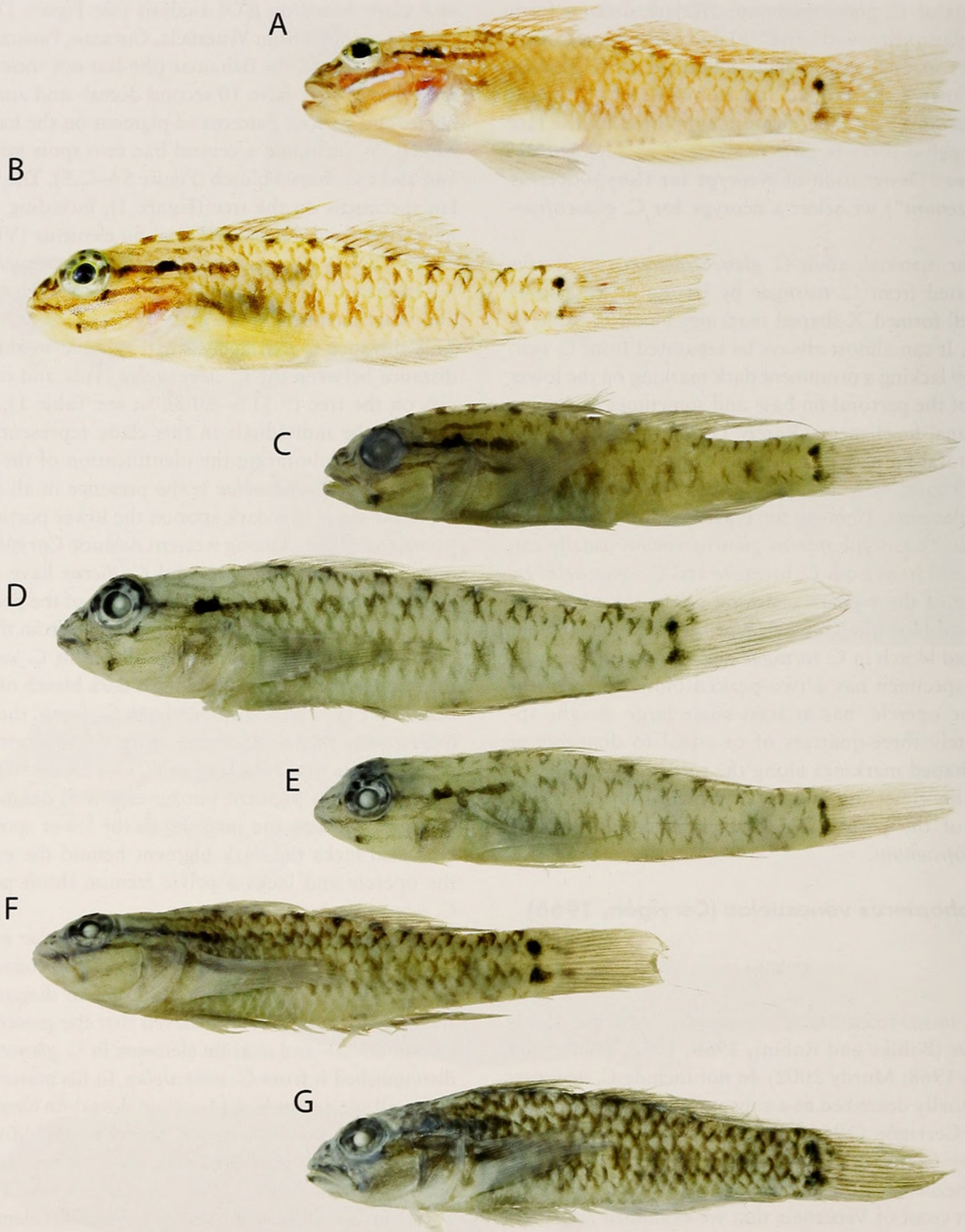


FIGURE 4. *Coryphopterus glaucofraenum*: A, Belize, 44 mm SL, DNA 6367; B, Belize, 25 mm SL, DNA 7352, USNM 394354; C, Belize, 35 mm SL, DNA 7351, USNM 394353, preserved; D, Venezuela, 31 mm SL, DNA 7744 2, AMNH 247339, alcohol preserved; E, Venezuela, 27 mm SL, DNA 7744 3, AMNH 247339, alcohol preserved; F, Panama, 34 mm SL, DNA 7712 2, AMNH 247335, alcohol preserved; G, Panama, 37 mm SL, DNA 7701 1, AMNH 247334, alcohol preserved.

several with 11 in both fins. There is thus more variability in numbers of second dorsal- and anal-fin elements than Cervigón indicated, and those fin-ray counts are of value in separating *C. glaucofraenum* and *C. venezuelae* only when 11 elements are present in both fins—a condition we have not observed in *C. glaucofraenum*, which may have 11 second dorsal-fin elements but no more than 10 anal-fin elements (see Table 2).

If a specimen has a dark blotch or triangle of pigment above the opercle, 11 second dorsal-fin *and* 11 anal-fin elements, and a prominent pigment spot on the lower portion of the pectoral-fin base, it is *C. venezuelae*.

If a specimen has those features and has 10 second dorsal- and anal-fin elements, it is usually *C. venezuelae* but could be *C. glaucofraenum*: as noted under "*Coryphopterus glaucofraenum*," rarely specimens of that species may have pigment on the ventral portion of the pectoral-fin base. The shape of the pigment marking above the opercle (with two peaks in *C. glaucofraenum*, a single triangular or rounded blotch in *C. venezuelae*; see "*Coryphopterus glaucofraenum*") will frequently resolve the species identification.

There are two distinct forms of *C. venezuelae* in terms of body pigment: one has at least some large X-shaped markings in the ventral row of markings similar to those of *C. glaucofraenum* (Figure 5B,D,E); the other is a much paler form, and the ventral pigment markings along the side of the body are usually fairly small, somewhat circular blotches (Figure 5A,C). Both forms, including the palest specimens, have a pigment spot on the lower pectoral-fin base, but this spot may be composed primarily of yellow chromatophores versus melanophores in pale specimens. The less-pigmented form is most easily confused with *C. tortugae*, but some of the pigment spots in the ventral row of *C. venezuelae* are usually more circular than the vertically elongate ones of *C. tortugae*. Additionally, none of our specimens of *C. tortugae* has a spot of pigment (yellow or black) on the ventral portion of the pectoral-fin base. Although unusually divergent intraspecifically in patterns of pigmentation (see Figure 5) relative to, for example, the very similar patterns between species such as *C. personatus* and *C. hyalinus*, the two forms of *C. venezuelae* form a tight genetic clade (intraspecific variation, 0.53%; see Figure 1, Table 1). The different pigment patterns do not correspond to different fin-ray counts, as we have observed 10 and 11 second dorsal- and anal-fin elements in both forms. For example, note the similar patterns of pigmentation in a specimen of *C. venezuelae* from Venezuela (Figure 5D) that has 11 second dorsal- and anal-fin elements and a specimen of *C. venezuelae* from Panama (Figure 5E) that has 10 second dorsal- and anal-fin elements. Furthermore, the differences are not attributable to sexual dimorphism or geography, but they could reflect differences in local habitat. Some specimens of *C. venezuelae* collected in mangrove areas tend to be dark, and those collected in reef areas pale, although we note that a dark form was collected on a reef off Panama (Figure 5E).

TABLE 2. Frequency distributions of numbers of second dorsal-fin and anal-fin elements in two species of *Coryphopterus*.

	No. of second dorsal-fin elements		No. of anal-fin elements		
Species	10	11	9	10	11
C. glaucofraenum	22	2	2	20	—
C. venezuelae	20	13	1	22	11

There is some correlation with size: the pale form of *C. venezuelae* is more common among small specimens (<30 mm standard length [SL]), and the form with prominent X-shaped markings is more common among larger specimens (>40 mm SL). Adults of the pale form of *C. venezuelae* (e.g., Figure 5A) look remarkably similar to juveniles (e.g., see Figure 7C). There is also a trend toward increasing depth of the head and anterior body in larger specimens. Similar differences in body shape and pigment with increasing size are evident in *C. glaucofraenum* (compare the juvenile in Figure 7B with adults in Figure 4). Possibly in *C. venezuelae*, growth is not always accompanied by a transformation in pigment and body depth, and adults retain more of the juvenile features. More investigation is needed to determine the relationships in *C. venezuelae* among pigment pattern, body shape, size, maturity, and local habitat. Cervigón (1966, 1994) did not illustrate any of his type specimens of *C. venezuelae*, but we obtained digital photographs of two of his paratypes (MOBR-P-0867 [Museo Oceanológico Hermano Benigno Román, Venezuela]; one is shown in Figure 6). The holotype is not in good condition (J. C. Capelo, MOBR, personal communication, 4 July 2008). The pigment of the paratypes most closely resembles that in Figure 5D herein: a triangular to rounded mark above the opercle, a roughly circular dark spot on the ventral pectoral-fin base, and two basicaudal spots joined by a light dusky bar. There is some evidence of X-shaped markings on the side of the body, but the body pigment is mostly faded. Cervigón (1966, 1994) did not mention X-shaped markings in his descriptions; rather, he noted that there are three longitudinal rows of dark spots.

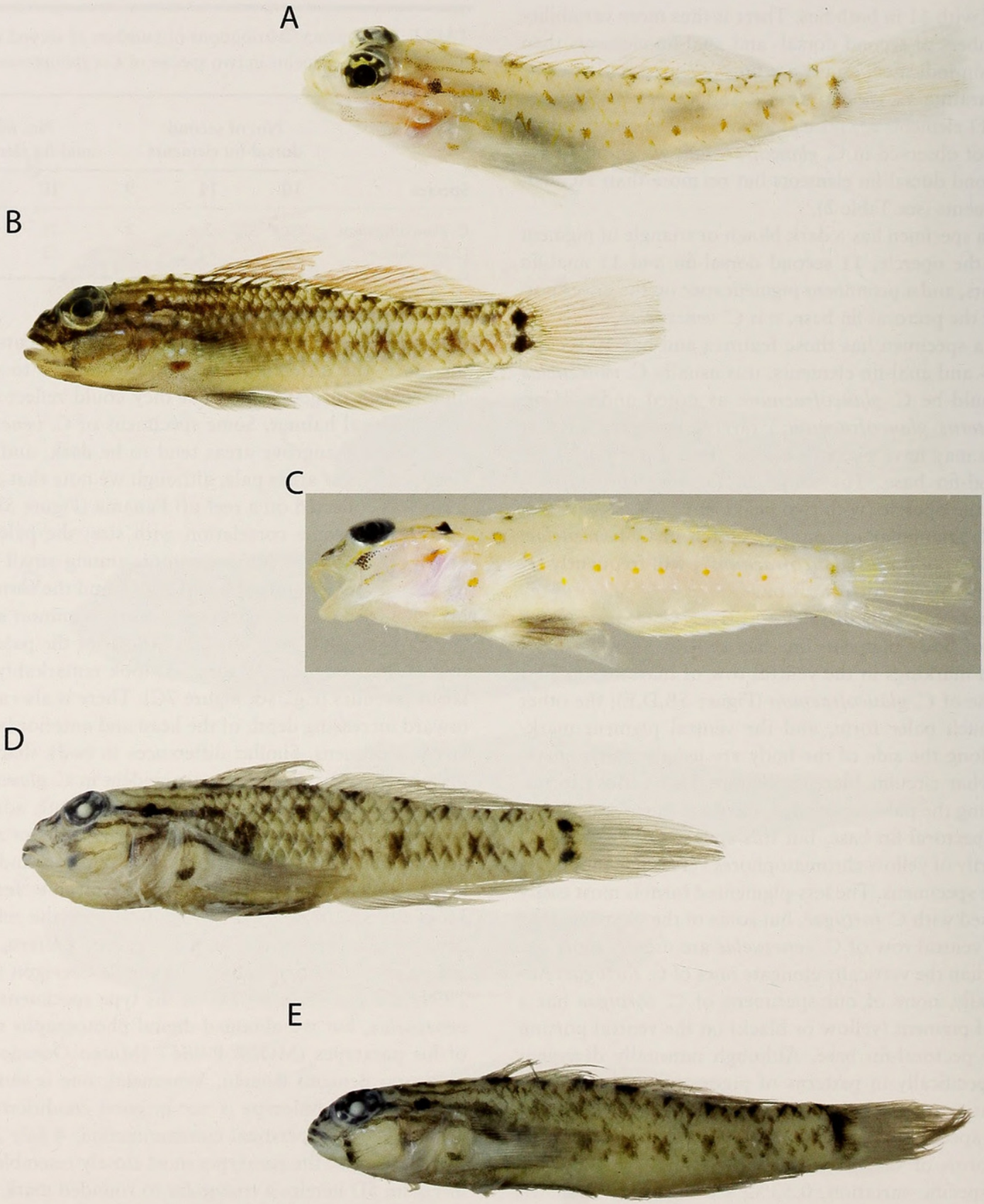


FIGURE 5. *Coryphopterus venezuelae*: A, Curacao, 29 mm SL, DNA 8260, USNM 394740; B, Venezuela, 54.4 mm SL, no DNA, Photo No. 1907 VT-05-530, photo by J. V. Tassell and D. R. Robertson; C, Belize, 35 mm SL, DNA 7248, USNM 394736; D, Venezuela, 50 mm SL, DNA JV15, AMNH 247345, alcohol preserved; E, Panama, 42.5 mm SL, DNA 7725-1, AMNH 247341, alcohol preserved.

Synonymy of *Coryphopterus bol*

Victor (2008) described *Coryphopterus bol* as a species that heretofore had been masquerading under *C. tortugae* (e.g., Garzón-Ferreira and Acero 1990:107, fig. 1A, Santa Marta specimens). We believe that Victor (2008) was correct in recognizing that the Santa Marta specimens are not *C. tortugae*, but our investigation indicates that they are *C. venezuelae*. The COI sequence that Victor (2008) provided for the new species (from the holotype from Puerto Rico) places it solidly with our *C. venezuelae* clade (PR SIO 0869, fig. 1). The average genetic distance between *C. bol* and individuals of *C. venezuelae* is 0.38% (range, 0.00%–0.85%) and, for comparison, the average genetic distance between the holotype of *C. bol* and the next most closely related clade (*C. tortugae*) is more than 20-fold greater, or 8.47% (range, 8.10%–9.21%). Diagnostic features of Victor's (2008:4) *C. bol* include 10 second dorsal- and anal-fin elements; 19 pectoral-fin rays; pelvic fins fully joined and with a distinct frenum; a prominent, dark, upward-pointed triangular marking on the stripe behind the eye; a discrete blotch of small melanophores on the lower third of the pectoral fin base; and a basicaudal marking that resembles a thick "C." The combination of the triangular marking on the stripe behind the eye above the opercle, the pigment blotch on the lower portion of the pectoral-fin base, and 10 second dorsal- and anal-fin elements matches most of our *C. venezuelae* specimens. Victor (2008) distinguished his new species from *C. venezuelae* based on the presence of 11 second dorsal- and anal-fin elements in *C. venezuelae*, but, as noted above (also see Table 2), specimens matching Cervigón's *C. venezuelae* based on the pre-pectoral pigment may have 10 or 11 second dorsal- and anal-fin elements.

Coryphopterus bol also matches *C. venezuelae* in number of pectoral-fin rays (19 in *C. bol*, 61% of specimens with 19 in Cervigón's [1994] *C. venezuelae* material), pelvic-fin morphology, and other pigment. For example, the basicaudal mark in *C. venezuelae* may be C-shaped, but it ranges in our material from two separate spots to a central bar of pigment (some examples are shown in Figure 5). The basicaudal pigment is also somewhat variable in the type material of *C. bol* (Victor, 2008:fig. 1). Two of the type specimens of *C. bol* most closely resemble the pale form of *C. venezuelae*; that is, the form with round spots on a relatively slender body (holotype and a 32.1-mm SL paratype). Two paratypes (24.5 and 29 mm SL) are darker and have at least some X-shaped markings. None of Victor's type material is larger than 32 mm SL, and, as noted under *C. venezuelae*, above, most of our dark, deeper-bodied specimens of *C. venezuelae* are >40 mm SL.

TABLE 3. Frequency distributions of the combinations of second dorsal-fin and anal-fin elements in *Coryphopterus venezuelae* by country.

	No. of second dorsal-fin elements / anal-fin elements				
Country	10/9	10/10	10/11	11/10	11/11
Belize	—	2	—	—	—
Curacao	1	11	1	1	—
Panama	—	6	1	—	—
Venezuela	—	2	—	1	9
Puerto Rico	—	1[a]	—	—	—

[a] Holotype of *Coryphopterus bol*.

In summary, one cannot distinguish *C. bol* and *C. venezuelae* on the basis of numbers of second dorsal- and anal-fin elements because there is more variation in those counts than previously reported. One might argue that specimens from Venezuela that have 11 elements in both the second dorsal and anal fins and heavy pigment with X-shape markings are *C. venezuelae* and that everything else in our *C. venezuelae* clade is *C. bol*. However, some specimens with those features, except with 10 elements in the second dorsal and anal fins, were taken in the same station off Venezuela as those with 11 elements (AMNH 247345 [American Museum of Natural History]), so would one identify the former as *C. venezuelae* or *C. bol*? Species identification of specimens with 11/10 or 10/11 second dorsal-/anal-fin elements also would be nebulous, as would species identification of dark forms with 10/10 but otherwise virtually identical to those with 11/11 (e.g., Figure 5D,E). Variation in COI among all specimens in the *C. venezuelae* clade is well within typical intraspecific levels for the genus. However, even if COI is masking recent divergence within the clade, there is a diagnostic morphological feature for the clade: a conspicuous spot or blotch of pigment on the lower pectoral-fin base; in combination with a triangular or circular blotch of pigment behind the eye above the opercle, this character is unique to *C. venezuelae*. The more common presence of 11 second dorsal- and anal-fin elements in some Venezuelan specimens may best be interpreted as regional variation. Known currently from Belize, Panama, Curacao, Venezuela, the Bahamas, the U.S. Virgin Islands, Puerto Rico, Saba, and Brazil, *C. venezuelae* appears to be a widespread species. It is misidentified in the USNM (U.S. National Museum;

FIGURE 6. Paratype of *Coryphopterus venezuelae*, MOBR-P-0867, 42 mm SL (length estimated from ruler included with original photograph; this is likely Cervigón's 41.2 mm SL paratype).

i.e., National Museum of Natural History, Smithsonian Institution)—and likely other museum collections—as *C. glaucofraenum* or *C. tortugae*.

Key Notes for *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae*

Juveniles (Figure 7), and occasionally adults, of *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* may lack the black marking or triangle above the opercle, or it is not as dark as other pigment in the stripe posterior to the eye. As we have used this feature in the "Revised Key to Western Atlantic *Coryphopterus*" (see below) to separate *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* from other species, absence of this feature in specimens of any of those species could present identification problems. If there are well-defined X's of pigment along the sides of the body (*C. glaucofraenum* and some *C. venezuelae*) or the basicaudal pigment comprises two spots or a dumbbell-shaped marking (most *C. glaucofraenum* and some *C. venezuelae*), users of the key should follow the option in the couplet that indicates the dark marking is present above the opercle (4b). If a specimen lacks the dark pigment spot above the opercle, has 11 second dorsal- and anal-fin rays, and has a prominent dark blotch on the lower portion of the pectoral-fin base, it can only be *C. venezuelae*. *Coryphopterus punctipectophorus* is similar in lacking the pigment spot above the opercle and having 11 second dorsal-fin elements, but it has 10 anal-fin elements (Springer, 1960). Furthermore, geography will currently separate those two species: *C. venezuelae* occurs in the Caribbean, and *C. punctipectophorus* is known only from the Gulf of Mexico and off the southeastern USA.

Coryphopterus dicrus Böhlke and Robins, 1960

FIGURE 8

Numerous features, in combination, separate *C. dicrus* from other western Atlantic *Coryphopterus*, including the following: no black ring of pigment around anus; no distinct dark spot behind eye above opercle; anal-fin elements 10; pelvic frenum absent; pectoral-fin base with two prominent dark spots of equal intensity, one above the other; and sides of body freckled with scattered large and smaller pigment blotches. The last two characters are the quickest way to make the identification. The only other species that usually have pigment dorsally *and* ventrally on the pectoral-fin base are *C. venezuelae* and *C. thrix*, but the dorsal pigment on the pectoral-fin base in *C. venezuelae*, when present, is a slash versus a spot, and the dorsal pigment on the pectoral-fin base in *C. thrix* is usually much more pronounced than the ventral marking. Additionally, both species have a pelvic frenum, which is lacking in *C. dicrus*.

Coryphopterus thrix Böhlke and Robins, 1960

FIGURE 8

Coryphopterus thrix is the only western Atlantic species of *Coryphopterus* that lacks black pigment around the anus *and* has the second dorsal-fin spine elongated into a filament. If the spine is broken, however, the species is still identifiable by the combination of features presented in the key, most notably the absence of a distinctive pigment blotch above the opercle, presence of a conspicuous dark blotch on the dorsal portion of the pectoral-fin base, and presence of a pelvic frenum.

Coryphopterus alloides Böhlke and Robins, 1960

FIGURE 9

Distinguishing features of *C. alloides* include having a low anal-fin count (8–9 total elements), a dark blotch of pigment on the lower portion of the membrane between the second and third dorsal spines, and the pelvic fins almost completely separate. Only *C. kuna*, among the *Coryphopterus* species lacking a black ring of pigment around the anus, has as few as 9 anal-fin elements, but that species has 9 second dorsal-fin elements and 15 pectoral rays (vs. usually 10 and 16–17, respectively, in *C. alloides*). *Coryphopterus kuna* may have a stripe and distal flag of pigment on the first dorsal fin, but it never has the pigment blotch on the lower portion of the first dorsal fin characteristic of *C. alloides*. The living color pattern of *C. alloides* is also distinctive: the head and anterior portion of the body bear a considerable amount of orange pigment, whereas the posterior portion of the body is yellow. An apparently cryptic species related to but genetically distinct from *C. alloides* and known only from Curacao is currently under investigation.

Key Note

In some preserved specimens of *C. alloides*, there are melanophores above the opercle that may lead the user of the key to select "4b. Distinct black blotch or triangle behind eye above opercle . . ." However, this pigment is never as consolidated and prominent in *C. alloides* as in

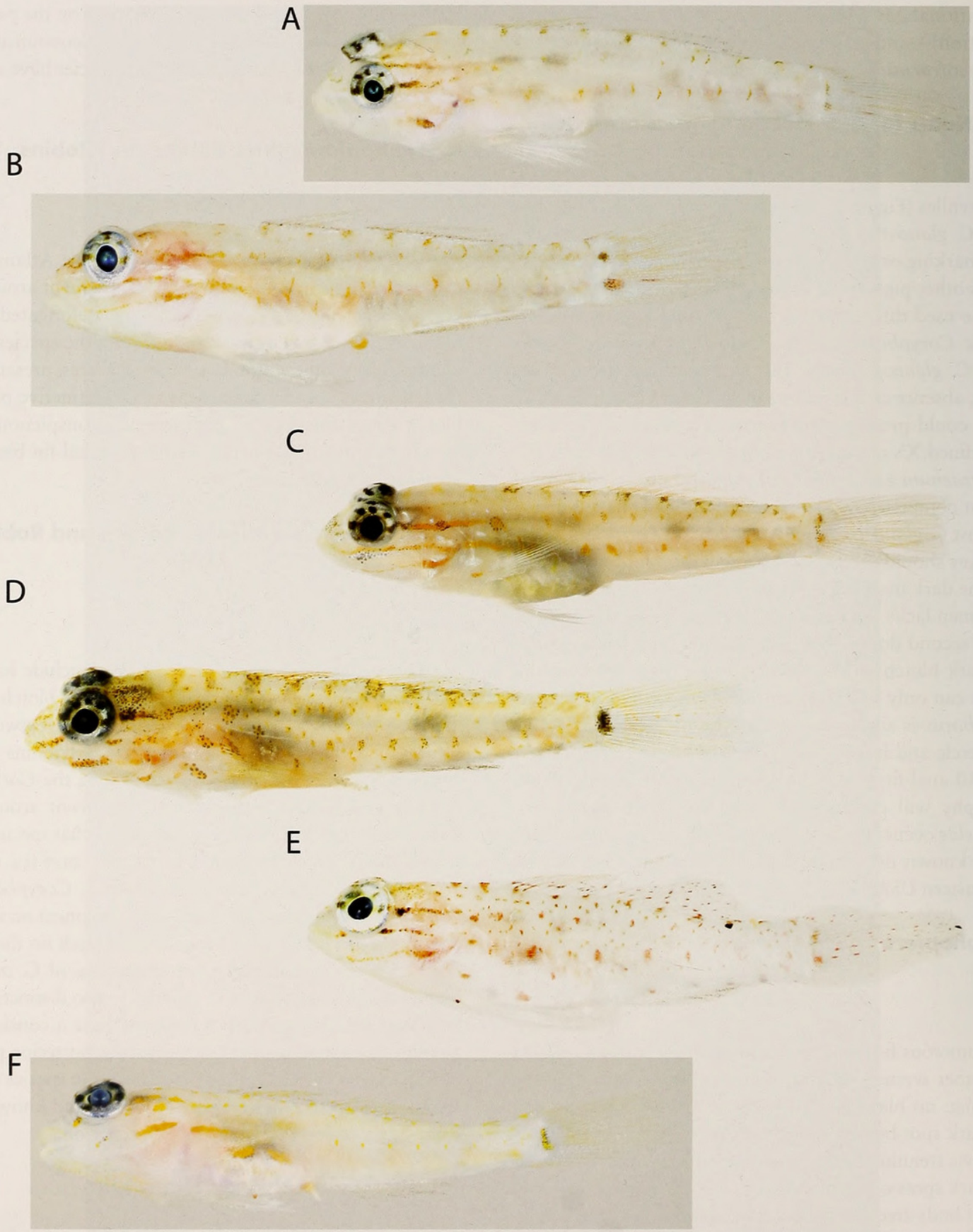


FIGURE 7. *Coryphopterus* juveniles: A, *C. tortugae*, Belize, 20 mm SL, DNA 7693, USNM 394800; B, *C. glaucofraenum*, Belize, 17 mm SL, DNA 7769, USNM 394793; C, *Coryphopterus venezuelae*, Belize, 17 mm SL, DNA 7728, USNM 394881, D, *Coryphopterus thrix*, Curacao, 16 mm SL, DNA 8261, USNM 394760; E, *Coryphopterus dicrus*, Belize, 13 mm SL, DNA 6110, USNM 394779. F, *Coryphopterus eidolon*, Belize, 18 mm SL, DNA 6223, USNM 394788.

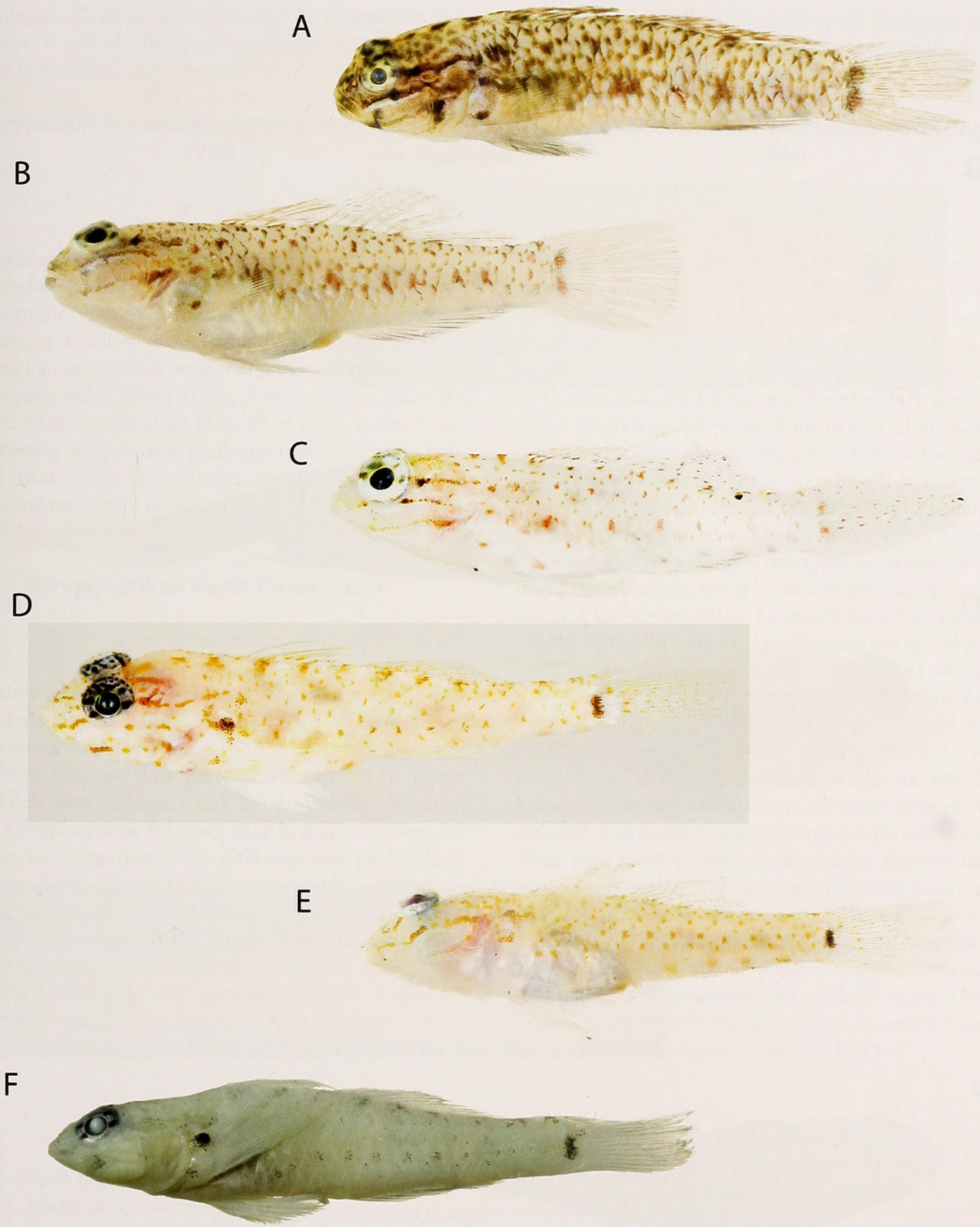


FIGURE 8. *Coryphopterus dicrus*: A, Florida, 38 mm SL, DNA 7348, USNM 394345; B, Curacao, 30 mm SL, DNA 8135, USNM 394747; C, Belize, 13 mm SL, DNA 6110, USNM 394779. *Coryphopterus thrix*: D, Belize, 23.5 mm SL, DNA 7816, USNM 394914; E, Curacao, 23 mm SL, DNA 8426, USNM 394761; F, Venezuela, AMNH 244983, 26 mm SL, alcohol preserved, no DNA.

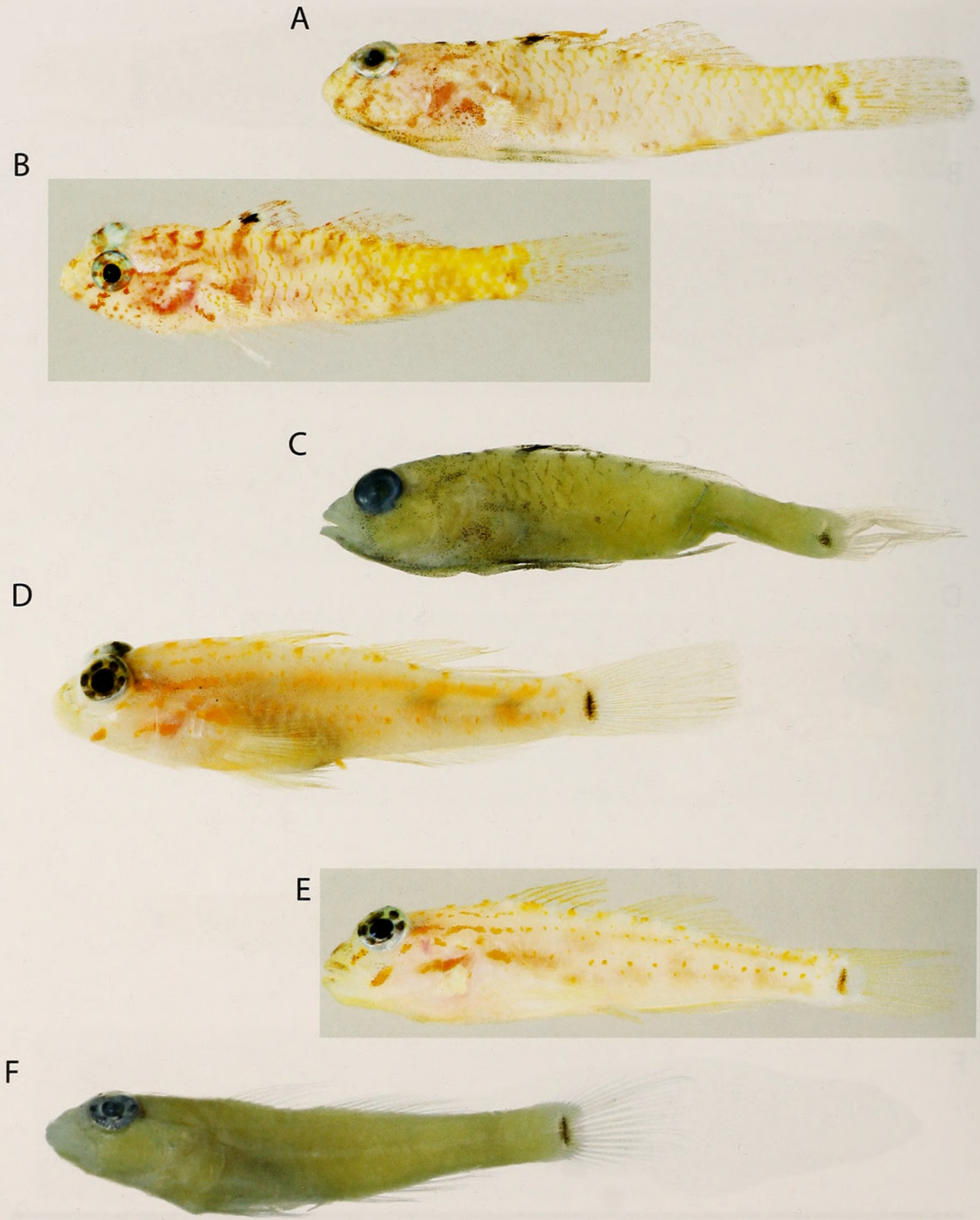


FIGURE 9. *Coryphopterus alloides*: A, Belize, 24 mm SL, DNA 7233, USNM 394754; B, Belize, 19 mm SL, DNA 7264, USNM 394755; C, Belize, 24 mm SL, preserved, DNA 7233, USNM 394754. *C. eidolon*: D, Curacao, 38 mm SL, DNA 8050, USNM 394885; E, Belize, 34 mm SL, DNA 7109, USNM 394752; F, Belize, 33 mm SL, preserved, DNA 5070, USNM 394750.

C. tortugae, *C. glaucofraenum*, and *C. venezuelae*; furthermore, *C. alloides* lacks a pelvic frenum, a conspicuous feature in the other three species.

Coryphopterus eidolon Böhlke and Robins, 1960

FIGURE 9

Pigment, except for basicaudal and scattered small body melanophores, is yellow, which disappears during preservation, typically rendering this a very pale goby. In life there is a yellow stripe behind the eye bordered by small melanophores that remain in preserved specimens after the color fades. There are no dark markings above the opercle, on the pectoral-fin base, or on the first dorsal fin. The absence of distinctive markings (other than the basicaudal mark) is the easiest way to recognize *C. eidolon*, a very abundant species in many of our samples, particularly from Belize and Curacao.

Coryphopterus kuna Victor, 2007

FIGURE 10

Baldwin and Smith (2003) described *Coryphopterus* B larvae from Belize as likely belonging to an unidentified species based on the low second dorsal- and anal-fin counts (9 in both fins) and low pectoral-fin count (15). Victor (2007) described *C. kuna*, which has the low fin-ray counts of the *Coryphopterus* B larvae, as a new species from off Panama. Incorporation of the COI sequence published in the original description of *C. kuna* into our analysis revealed that *Coryphopterus* B larvae are *C. kuna*. This species is distinctive in typically having 9 second dorsal- and anal-fin elements, as well as a low pectoral-ray count of 15 (found elsewhere only in *C. personatus* and *C. hyalinus*). Apparently a small fish—the adult male holotype is 17.1 mm SL—*C. kuna* has little dark pigment: numerous small spots on the pelvic fin of the holotype, a few scattered small spots on the sides of the body, no markings on the pectoral-fin base, and no basicaudal spot. It lacks a pelvic frenum.

Coryphopterus punctipectophorus Springer, 1960

FIGURE 10

Coryphopterus punctipectophorus is similar to *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae* in having three rows of pigment spots along the side of the body, but it differs from those species in lacking a dark blotch or triangle behind the head above the opercle. It is most similar to *C. venezuelae* in having a prominent dark spot on the lower portion of the pectoral-fin base, and juvenile (and occasionally adult) specimens of *C. venezuelae* that lack the pigment blotch above the opercle will typically key to *C. punctipectophorus* based on the ventral pigment spot on the pectoral-fin base. Like *C. venezuelae*, *C. punctipectophorus* was originally described as having 11 second dorsal-fin elements, but as noted above (see *C. venezuelae*), the former has 10 or 11 second dorsal elements. The "dusky light buff" pigment spots along the dorsal contour and "coral pink" spots along the sides of the body in fresh material of *C. punctipectophorus* (Springer, 1960:240; see Figure 10B,E herein) apparently fade in preserved material (see Figure 10D). The known distribution of *C. punctipectophorus* includes both coasts of Florida, the Gulf of Mexico (including the southern Gulf where it meets the Caribbean), and South Carolina. It apparently inhabits deeper water than some *Coryphopterus* species: the type material was collected at 62 and 120 feet. It has not been reported from the Caribbean. We have not collected *C. punctipectophorus*, and fresh material of the species was not available for inclusion in our genetic analysis. Thacker and Cole's (2002) *C. punctipectophorus* from Belize (GenBank Accession No. AF391396) is *C. dicrus*, based on incorporation of their COI sequence into our data set.

REVISED KEY TO THE WESTERN ATLANTIC SPECIES OF *CORYPHOPTERUS*

1a. Black ring of pigment surrounding anus 2
1b. Black ring around anus absent 4
2a. One interorbital pore anteriorly 3
2b. Two interorbital pores anteriorly . . . . . *Coryphopterus hyalinus*
3a. Second dorsal and anal fins each typically with 11 total elements; head with some orange pigment in life; body translucent, with several squares or rectangles of pale orange pigment internally; preserved specimens lacking conspicuous postorbital stripes of melanophores but with "mask" of pigment around eye . . . . . *Coryphopterus personatus*

(continued on p. 130)

REVISED KEY TO THE WESTERN ATLANTIC SPECIES OF *CORYPHOPTERUS* *(continued)*

3b. Second dorsal and anal fins typically with 10 total elements; head and body predominantly yellow in life; a dusky internal stripe along posterior section of vertebral column; preserved specimens with postorbital stripes of melanophores and scattered spots over entire body ..... ***Coryphopterus lipernes***

4a. No distinct black blotch behind eye above opercle in adults; pigment above opercle, if present, no larger or darker than other markings behind eye; pelvic frenum present or absent (see "Key Note" for *C. alloides* in text) *5*

4b. Distinct black blotch or triangle behind eye above opercle in adults, blotch usually larger and darker than other pigment in stripe behind eye; pelvic frenum present (see "Key Notes for *C. tortugae*, *C. glaucofraenum*, and *C. venezuelae*" in text) 10

5a. Anal-fin elements 8–9 (usually 9), pectoral-fin rays 15–17, pelvic frenum absent *6*

5b. Anal-fin elements 10–11, pectoral-fin rays 17–20, pelvic frenum present or absent *7*

6a. Second dorsal and anal fins each with 9 elements; pectoral-fin rays 15; pelvic fins fully joined; first dorsal fin with stripe of black pigment; in life, head and body with orange spots and blotches and sometimes with flag of dark pigment on 1st–3rd dorsal spines ..... ***Coryphopterus kuna***

6b. Second dorsal fin with 10 elements, anal fin with 9 (rarely 8); pectoral-fin rays 16–17; pelvic fins almost completely separate; black blotch or bar between 2nd and 3rd dorsal spines; head and anterior body mottled orange in freshly caught specimens, posterior body mottled yellow ..... ***Coryphopterus alloides***

7a. Pectoral-fin base with two prominent dark spots of equal intensity, one *dorsally* and one *ventrally*; upper spot usually with swath of melanophores extending posteriorly onto pectoral-fin rays; sides of body freckled with scattered large and smaller blotches of melanophores (blotches associated with coral, tan, yellow pigment in life); pelvic frenum absent ..... ***Coryphopterus dicrus***

7b. Pectoral-fin base not with two prominent dark spots (or, if two spots present, upper spot more intense); sides of body with few dark markings (with few to many yellow spots in life) or with three rows of light markings (coral pink/orange in life); pelvic frenum present *8*

8a. Pectoral-fin base without prominent dark markings but sometimes with a few to many scattered melanophores; sides of body with few if any dark markings (with yellow spots in life) except for basicaudal spot ..... ***Coryphopterus eidolon***

8b. Pectoral-fin base with prominent markings; sides of body with or without numerous dark markings *9*

9a. Pectoral-fin base with distinct pigment spot *dorsally*, spot usually dark above, diffuse below, often with dots trailing ventrally; ventral dots coalescing into a separate spot in some specimens (ventral spot, if present, less intense than dorsal spot); second dorsal-fin elements 9–10; second dorsal spine filamentous ..... ***Coryphopterus thrix***

9b. Pectoral-fin base with prominent dark spot or blotch only on *ventral* portion; second dorsal-fin elements 11; second dorsal spine not filamentous ..... ***Coryphopterus punctipectophorus***

10a. Body usually pale, pigment primarily comprising three rows of markings on side of body; lower row comprising small, mostly vertically elongate markings, some of which may be crescent shaped or some part of an X-shape but rarely well-defined X's; if X-shaped markings present, their height is considerably shorter than eye diameter; pigment marking above opercle usually a triangle, and basicaudal pigment usually a central bar ..... ***Coryphopterus tortugae***

10b. Body heavily pigmented or pale but without vertically elongate or crescent-shaped markings in ventral row of pigment on side of body; height of X-shaped markings, if present, three-quarters of or equal to diameter of eye; pigment marking above opercle triangular, rounded, or with two peaks; basicaudal pigment comprising two separate spots, two spots connected by a line of pigment and resembling a dumbbell, a central bar, or a C-shaped marking *11*

11a. Pigment on pectoral-fin base variable but always with dark spot or rectangular-shaped blotch ventrally (may be associated with bright yellow pigment in life); one or two additional bars, blotches, or concentrations of pigment sometimes present dorsally; three rows of dark markings on side of body, some in lower row large, X-shaped markings in heavily pigmented specimens, small, circular blotches in paler specimens; pigment marking above the opercle triangular or round ..... ***Coryphopterus venezuelae***

11b. Pectoral-fin base rarely with prominent dark marking ventrally, although melanophores may form one to three light to moderate concentrations on base; body with three rows of dark markings, most of those in the lower row large, distinctive X-shaped markings; pigment marking above opercle usually with two well-defined peaks ..... ***Coryphopterus glaucofraenum***

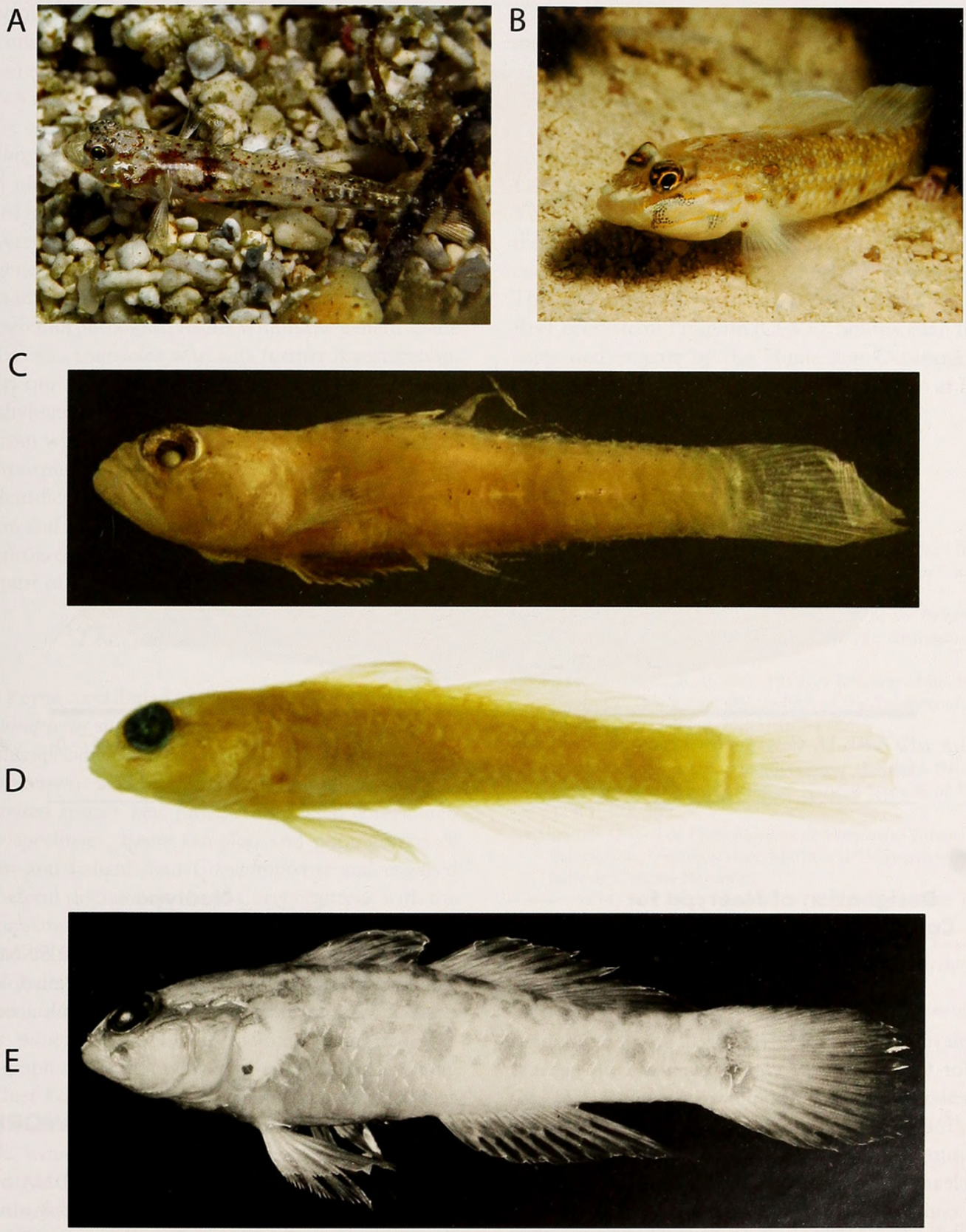


FIGURE 10. A, *Coryphopterus kuna*, San Andres, Colombian Caribbean (photo by Keri Wilk, ReefNet Inc.); B, *Coryphopterus punctipectophorus*, Holbox Island, Mexico (photo by Hilario Itriago); C, *Coryphopterus kuna*, Panama, 17.1 mm SL, holotype, SIO-07-5, preserved, DNA GB EF55021 (reproduced from B. Victor, 2007, fig. 1A, *Zootaxa* 1526:53); D, *Coryphopterus punctipectophorus*, South Carolina, 28 mm SL, USNM 315530, preserved, no DNA; E, *Coryphopterus punctipectophorus*, Florida, Gulf of Mexico, 42 mm SL, holotype, ANSP 90103, preserved, no DNA.

FIGURE 11. *Coryphopterus glaucofraenum*, neotype, USNM 393907, Belize, 44 mm SL, DNA 6367: A, fresh; B, preserved.

Designation of Neotype for *Coryphopterus glaucofraenum*

FIGURE 11

Eschmeyer (2008) noted the need for designating a neotype for *Coryphopterus glaucofraenum* Gill, because the whereabouts of the holotype are unknown. He also noted that four MCZ specimens assumed to be syntypes do not constitute type material because Gill's (1863) description was clearly based on a single specimen. Because of the historical confusion regarding the validity of *C. tortugae* and *C. venezuelae* as distinct from *C. glaucofraenum*, and because the three species can be difficult to separate, we have elected to designate a neotype for *C. glaucofraenum* from which we have successfully obtained a COI sequence that places the specimen in the *C. glaucofraenum* clade. We hereby make the following type designation:

Neotype

Coryphopterus glaucofraenum Gill, USNM 393907, 44 mm SL, DNA 6367, Twin Cays, Belize, mangrove edge on interior channel, 0–6 ft. (GenBank accession no. GQ367355.)

SUMMARY AND FUTURE WORK

Cytochrome *c* oxidase I sequences (DNA barcoding) were useful in determining the number of distinct genetic lineages within Caribbean *Coryphopterus*. We used the neighbor-joining tree (see Figure 1) derived from those sequences to assemble voucher specimens (and color photographs of them taken before preservation) into clades and then compared the morphology of specimens among those clades. Assigning clades to species was relatively easy based

on review of original literature and examination of some type specimens (or photographs of them). Resolving the identities of many Caribbean *Coryphopterus* in the absence of the DNA data would have been extremely difficult.

We are continuing to expand our geographic coverage of *Coryphopterus* sampling and will continue sequencing COI, and ultimately other genes, from specimens from a diversity of locations. The precise geographic distributions of most western Atlantic *Coryphopterus* are not known, and our genetic analyses have revealed the presence of one or more additional cryptic species. Additionally, the existence of two morphological forms within the genetic clade identified as *C. venezuelae* warrants further investigation. Ultimately, our multi-locus data set will enable us to reanalyze phylogenetic relationships among *Coryphopterus* species, from which we can investigate patterns of speciation and morphological divergence. Finally, testing of the species identifications of *Coryphopterus* larvae proposed by Baldwin and Smith (2003) based on morphology is currently in progress based on COI sequences of larvae collected as part of this study.

Acknowledgments

Cody Payne contributed to the organization of our Belizean *Coryphopterus* material, made radiographs and counts of numerous specimens, helped distinguish *C. tortugae* from *C. glaucofraenum*, and provided data helpful in developing the revised species key. James Van Tassell contributed numerous specimens, tissue samples, and photographs of Venezuelan and Panamanian *Coryphopterus* and engaged in many helpful discussions about *Coryphopterus* with the first author. Amy Driskell and Andrea Ormos provided laboratory and logistical assistance. Jon Fong provided images of the holotype of *Ctenogobius tortugae*. Victor Springer, Lisa Palmer, and Hilario Itriago provided images of *Coryphopterus punctipectophorus*. Benjamin Victor provided the photograph of the holotype of *C. kuna*, and Zhi-Qiang Zhang, Chief Editor of *Zootaxa*, allowed us to reproduce this image. Keri Wilk provided the in situ image of *C. kuna*. Annemarie Kramer allowed us to include her sequences of *C. tortugae* from Curacao in our analysis. Oscar M. Lasso-Alcala, Juan C. Capelo, and Ramon Varela provided digital images of two paratypes of *C. venezuelae*. Michael Carpenter, Zachary Foltz, Amy Driskell, and Justin Bagley provided field assistance in Belize and Florida. Research in Florida was conducted pursuant to Special Activity License 07SR-1024. Amos Gazit, Kate Wilson, and Maureen Kunen made it possible for us to collect fish samples through the CARMABI laboratory in Curacao. Fieldwork in the Bahamas was conducted under the auspices of the Perry Institute of Marine Science, with logistical assistance from Brenda Gadd. Fourteen members of the first author's family contributed to the fieldwork in the Bahamas, and a portion of that work was funded by a generous donation from Christine B. Lang in memory of David E. Baldwin and Richard A. Lang. The Smithsonian Marine Science Network provided most of the funding for fieldwork, and the Smithsonian DNA Barcoding Initiative provided funding for molecular analyses. This is contribution number 837 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund, and Smithsonian Marine Station at Fort Pierce (SMSFP) Contribution No. 756.

LITERATURE CITED

Baldwin, C. C., and D. G. Smith. 2003. Larval Gobiidae (Teleostei: Perciformes) of Carrie Bow Cay, Belize, Central America. *Bulletin of Marine Science*, 72:639–674.

Böhlke, J. E., and C. G. Chaplin. 1968. *Fishes of the Bahamas and Adjacent Tropical Waters*. Wynnewood, Pa.: Livingston Publishing Company.

Böhlke, J. E., and C. R. Robins. 1960. A Revision of the Gobioid Fish Genus *Coryphopterus*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 112(5):103–128.

———. 1962. The Taxonomic Position of the West Atlantic Goby, *Eviota personata*, with Descriptions of Two New Related Species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 114(5):175–189.

Cervigón, F. 1966. *Los Peces Marinos de Venezuela*. Volume II. Caracas: Estacion de Investigaciones Marinas de Margarita Fundacion La Salle de Ciencias Naturales.

———. 1994. *Los Peces Marinos de Venezuela*. Volume III. Caracas: Fundación Cientifica Los Roques.

Eschmeyer, W. N., ed. 2008. *Catalog of Fishes: Electronic Version* (updated 23 April 2008), http://www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html (accessed January 2008).

Garzón-Ferreira, J., and A. P. Acero. 1990. Redescription of *Coryphopterus tortugae* (Jordan) (Osteichthyes: Gobiidae), a Valid Species of Goby from the Western Atlantic. *Northeast Gulf Science*, 11(2):105–112.

Gill, T. N. 1863. Descriptions of the Gobioid Genera of the Western Coast of Temperate North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 15:262–267.

Greenfield, D. W., and R. K. Johnson. 1999. Assemblage Structure and Habitat Associations of Western Caribbean Gobies (Teleostei: Gobiidae). *Copeia*, 1999(2):251–266.

Jordan, D. S. 1904. Notes on the Fishes Collected in the Tortugas Archipelago. *Bulletin of the U.S. Fish Commission*, 22(1902): 539–544.

Jordan, D. S., and J. C. Thompson. 1905. The Fish Fauna of the Tortugas Archipelago. *Bulletin of the Bureau of Fisheries*, 24:229–256.

Kimura, M. 1980. A Simple Method for Estimating Evolutionary Rates of Base Substitutions Through Comparative Studies of Nucleotide Sequences. *Journal of Molecular Evolution*, 16:111–120.

Longley, W. H., and F. Hildebrand. 1941. *Systematic Catalogue of the Fishes of Tortugas, Florida: With Observations on Color, Habits, and Local Distribution*. Washington, D.C.: Carnegie Institution of Washington.

Murdy, E. O. 2002. "Gobiidae." In *The Living Marine Resources of the Western Central Atlantic. Volume 3: Bony Fishes, Part 2 (Opistognathidae to Molidae), Sea Turtles and Marine Mammals*, ed. K. E. Carpenter, pp. 1375–2127. Rome: The Food and Agriculture Organization of the United Nations.

Saitou, N., and M. Nei. 1987. The Neighbor-Joining Method: A New Method for Reconstructing Phylogenetic Trees. *Molecular Biology and Evolution*, 4:406–425.

Seutin, G., B. N. White, and P. T. Boag. 1990. Preservation of Avian Blood and Tissue Samples for DNA Analysis. *Canadian Journal of Zoology*, 69:82–90.

Smith, C. L., J. C. Tyler, W. P. Davis, R. S. Jones, D. G. Smith, and C. C. Baldwin. 2003. *Fishes of the Pelican Cays, Belize*. Atoll Research Bulletin, No. 497. Washington, D.C.: National Museum of Natural History, Smithsonian Institution.

Springer, V. G. 1960. A New Gobiid Fish from the Eastern Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean*, 10(2):237–240.

Swofford, D. L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods)*. Version 4, Beta 10 (CD-Rom). Sunderland, Mass.: Sinauer Associates.

Thacker, C. E., and K. S. Cole. 2002. Phylogeny and Evolution of the Gobiid Genus *Coryphopterus*. *Bulletin of Marine Science*, 70(3):837–850.

Victor, B. C. 2007. *Coryphopterus kuna*, a New Goby (Perciformes: Gobiidae: Gobiinae) from the Western Caribbean, with the Identification of the Late Larval Stage and an Estimate of the Pelagic Larval Duration. *Zootaxa*, 1526:51–61.

———. 2008. Redescription of *Coryphopterus tortugae* (Jordan) and a New Allied Species *Coryphopterus bol* (Perciformes: Gobiidae: Gobiinae) from the Tropical Western Atlantic Ocean. *Journal of the Ocean Science Foundation*, 1:1–19.

APPENDIX

TABLE A.1. *Coryphopterus* material. A number in the DNA column indicates that the specimen was analyzed for cytochrome *c* oxidase 1. An asterisk beside this number indicates the entry appears in the neighbor-joining tree in Figure 1; because of space constraints, not all specimens for which DNA was successfully sequenced are included in Figure 1. Extracting DNA was not attempted on formalin-fixed specimens. If the specimen was not sampled for DNA, "no DNA" is recorded in this column; BZE, Belize; FLA, Florida; CUR, Curacao; BAH, Bahamas; PAN, Panama; VEN, Venezuela.

Species	DNA	Standard length (mm)	Specimen voucher [a]	Photo voucher at NMNH
C. lipernes	BZE 4067*	—	No voucher	No
	BZE 4082*	23	No voucher	No
	BZE 4083*	21	No voucher	No
	BZE 7729*	18	USNM 394796	Yes
	CUR 8051*	21	USNM 394895	Yes
	CUR 8326*	20	USNM 394896	Yes
	CUR 8327*	17	USNM 394894	Yes
C. hyalinus	BZE 4511*	15	No voucher	No
	BZE 4512*	15	No voucher	No
	BZE 5066*	13	No voucher	Yes
	BZE 6221*	13.5	USNM 394795	Yes
	BZE 6222*	14.5	USNM 394794	Yes
	BZE 7760*	7	No voucher	Yes
	CUR 8044*	20	USNM 394890	Yes
	CUR 8046*	19.5	USNM 394891	Yes
	CUR 8264*	19	USNM 394893	Yes
	CUR 8265*	17	USNM 394889	Yes
	CUR 8266*	16.5	USNM 394892	Yes
C. personatus	BZE 4014*	—	No voucher	No
	BZE 4079*	19	No voucher	Yes
	BZE 4307*	24	USNM 394756	Yes
	BZE 4308*	21	USNM 394757	Yes
	BZE 4309*	18	USNM 394758	Yes
	BZE 5067*	19	USNM 394913	Yes
	BZE 7163*	15	USNM 394742	Yes
	CUR 8045*	19.5	USNM 394897	Yes

Species	DNA	Standard length (mm)	Specimen voucher [a]	Photo voucher at NMNH
	BAH 8263	23	USNM 394904	Yes
	BAH 8264*	22	USNM 394905	Yes
	PAN 7712-1*	22	AMNH 247346	No
	PAN 7712-5*	22	AMNH 247346	No
C. tortugae	BZE 4016*	28	No voucher	Yes
	BZE 4530*	40	USNM 394730	Yes
	BZE 5237*	34	USNM 394743	Yes
	BZE 5238*	30	USNM 394731	Yes
	BZE 7106*	20	USNM 394732	Yes
	BZE 7107*	36	USNM 394733	Yes
	BZE 7333*	25	USNM 394744	Yes
	BZE 7677*	31	USNM 394801	Yes
	BZE 7690	37	USNM 394878	Yes
	BZE 7691*	29	USNM 394802	Yes
	BZE 7692*	36	USNM 394879	Yes
	BZE 7693*	20	USNM 394800	Yes
	BZE 7708*	33	USNM 394877	Yes
	BZE 7709*	29	USNM 394798	Yes
	BZE 7734*	26	USNM 394799	Yes
	BZE (no DNA)	40	USNM 329834	No
	BZE (no DNA)	33	USNM 334838	No
	CUR CG25*	—	No voucher	No
	CUR CG26*	—	No voucher	No
	PAN 7725-6*	36	AMNH 247347	No
	VEN (no DNA)	45	USNM 194103	No
	VEN 7736-1*	33	AMNH 247340	No
	VEN 7736-4*	37	AMNH 247340	No
	VEN 7736-6*	46	AMNH 247340	No
	Bermuda (no DNA)	9 (15–31)	USNM 330023	No
	FLA (no DNA, photo of holotype)	—	SU 08363	No
C. glaucofraenum	BZE 6037*	35	USNM 394347	Yes
	BZE 6367*	44	USNM 393907	Yes
	BZE 7343*	6	No voucher	Yes
	BZE 7351*	35	USNM 394353	Yes
	BZE 7352*	25	USNM 394354	Yes
	BZE 7353*	17.5	USNM 394355	Yes
	BZE 7733*	25	USNM 394748	Yes
	BZE 7768*	22	USNM 394792	Yes
	BZE 7769*	17	USNM 394793	Yes
	BZE 7796*	8.5	No voucher	Yes
	BZE 7798*	8.5	No voucher	Yes
	FLA 7341	49	USNM 394348	Yes
	FLA 7342	42	USNM 394349	Yes
	FLA 7343*	35	USNM 394350	Yes
	FLA 7344	36	USNM 394351	Yes
	FLA 7345	30	USNM 394352	Yes
	FLA 7674	49	USNM 394356	Yes
	FLA 7675	44	USNM 394357	Yes
	FLA 7676	38	USNM 394358	Yes
	FLA 7677	32	USNM 394729	Yes
	PAN 7701-1*	39	AMNH 247334	No
	PAN 7701-2*	40.5	AMNH 247334	No
	PAN 7701-3*	32	AMNH 247334	No
	PAN 7701-4*	26.5	AMNH 247334	No
	PAN 7701-5*	33	AMNH 247334	No
	PAN 7712-2*	35	AMNH 247335	No

continued

TABLE A.1. *continued*

Species	DNA	Standard length (mm)	Specimen voucher [a]	Photo voucher at NMNH
	VEN 7729-1*	31	AMNH 247336	No
	VEN 7729-2*	30	AMNH 247336	No
	VEN 7729-3*	31	AMNH 247336	No
	VEN 7736-2*	37.5	AMNH 247337	No
	VEN 7738-1*	38	AMNH 247338	No
	VEN 7738-2*	36	AMNH 247338	No
	VEN 7738-3*	39	AMNH 247338	No
	VEN 7744-2*	32	AMNH 247339	No
	VEN 7744-3*	27	AMNH 247339	No
	VEN 7744-4*	28.5	AMNH 247339	No
	Bahamas (no DNA)	31	USNM 386863	No
	Bahamas (no DNA)	2 (30–32)	USNM 386955	No
	Bermuda (no DNA)	4 (27–35)	USNM 178908	No
	Bermuda (no DNA)	2 (45–46)	USNM 178555	No
C. venezuelae	BZE 5099*	16	USNM 394735	Yes
	BZE 5319*	8.5	No voucher	Yes
	BZE 7248*	35	USNM 394736	Yes
	BZE 7362*	7.5	No voucher	Yes
	BZE 7704*	20	USNM 394880	Yes
	BZE 7728*	17	USNM 394881	Yes
	BZE 7797*	8.5	No voucher	Yes
	CUR 8052*	30.5	USNM 394737	Yes
	CUR 8053*	30	USNM 394764	Yes
	CUR 8054*	26.5	USNM 39475	Yes
	CUR 8055	28	USNM 394766	Yes
	CUR 8208*	31.5	USNM 394738	Yes
	CUR 8259*	29	USNM 394739	Yes
	CUR 8260*	29	USNM 394740	Yes
	CUR 8427*	35	USNM 394741	Yes
	BAH 8048*	43	USNM 394908	Yes
	BAH 8049*	42	USNM 394906	Yes
	BAH 8262*	39	USNM 394909	Yes
	PAN 7725-1*	42.5	AMNH 247341	No
	PAN 7725-2*	38	AMNH 247341	No
	PAN 7725-3*	33	AMNH 247341	No
	PAN 7725-4*	39	AMNH 247341	No
	PAN 7725-5*	42.5	AMNH 247341	No
	VEN 6670-3*	41	AMNH 247342	No
	VEN 6670-4*	45	AMNH 247342	No
	VEN 7733-1*	29	AMNH 247343	No
	VEN JV07*	20	AMNH 247344	No
	VEN JV08*	29.5	AMNH 247344	No
	VEN JV09*	36	AMNH 247345	No
	VEN JV10*	29	AMNH 247345	No
	VEN JV11*	29	AMNH 247345	No
	VEN JV12*	52	AMNH 247345	No
	VEN JV13*	50	AMNH 247345	No
	VEN JV14*	50	AMNH 247345	No
	VEN JV15*	50	AMNH 247345	No
	VEN JV16*	29	AMNH 247345	No
	VEN (no DNA; photo of paratype)	~42	MOBR-P-0867	No
	Puerto Rico; holotype of *C. bol** (DNA from Victor, 2008)	26.8	SIO 0869	No
	Saba (no DNA)	15	USNM 387726	No

Species	DNA	Standard length (mm)	Specimen voucher [a]	Photo voucher at NMNH
	Brazil	4 (2–39)	USNM 357709	No
C. dicrus	BZE 4213*	22	USNM 394337	Yes
	BZE 5239*	27	USNM 394763	Yes
	BZE 6274*	25	USNM 394774	Yes
	BZE 6110*	13	USNM 394779	Yes
	BZE 7238	29	USNM 294338	Yes
	BZE 7266	24	USNM 294339	Yes
	BZE 7354*	22	USNM 394745	Yes
	BZE 7410	27	USNM 394746	Yes
	BZE 7700*	19	USNM 394778	Yes
	BZE 7701*	17	USNM 394776	Yes
	BZE 7707*	21	USNM 394777	Yes
	BZE 7745*	23	USNM 394780	Yes
	BZE 7818*	22	USNM 394775	Yes
	FLA 7346*	43	USNM 394343	Yes
	FLA 7347*	41	USNM 394344	Yes
	FLA 7348*	38	USNM 394345	Yes
	FLA 7680	39	USNM 394340	Yes
	FLA 7681	42	USNM 394341	Yes
	FLA 7682	44	USNM 394342	Yes
	CUR 8135*	30	USNM 394747	Yes
	BAH 8134*	43	USNM 394900	Yes
	BAH 8135*	38	USNM 394898	Yes
	BAH 8232	36	USNM 394899	Yes
	VEN 7736-3*	35	AMNH 247332	No
	VEN JV01*	33	AMNH 247333	No
	VEN JV02*	35	AMNH 247333	No
	VEN JV03*	36	AMNH 247333	No
	VEN JV04*	20.5	AMNH 247333	No
	VEN JV05*	21	AMNH 247333	No
	VEN JV06*	20	AMNH 247333	No
	Saba (no DNA)	4 (25–28)	USNM 388525	No
	Tobago (no DNA)	35	USNM 318808	No
	Tobago (no DNA)	3 (23–25)	USNM 318818	No
	Dominica (no DNA)	11 (13–27)	USNM 325165	No
C. thrix	BZE 6111*	15	USNM 394797	Yes
	BZE 7265*	10	USNM 394734	Yes
	BZE 7267*	30	USNM 394759	Yes
	BZE 7816*	23	USNM 394914	Yes
	BZE 7817*	22	USNM 394915	Yes
	BZE (no DNA)	3 (20–28.5)	USNM 328240	No
	CUR 8261*	16	USNM 394760	Yes
	CUR 8426*	23	USNM 394761	Yes
	Venezuela (no DNA)	26	AMNH 244983	No
	Navassa (no DNA)	31	USNM 359403	No
	Tobago (no DNA)	32	USNM 318811	No
	Tobago (no DNA)	2 (23–24)	USNM 317133	No
C. eidolon	BZE 4017*	31	USNM 394749	Yes
	BZE 4080*	20	USNM	Yes
	BZE 4081*	29	No voucher	No
	BZE 4089*	–	No voucher	No
	BZE 5070*	33	USNM 394750	Yes
	BZE 5099	16	No voucher	Yes
	BZE 6223*	18	USNM 394788	Yes
	BZE 6224*	24	USNM 394789	Yes
	BZE 6246*	25	USNM 394787	Yes
	BZE 6268*	23.5	USNM 394790	Yes
	BZE 6302*	33	USNM 394751	Yes

continued

TABLE A.1. *continued*

Species	DNA	Standard length (mm)	Specimen voucher [a]	Photo voucher at NMNH
	BZE 7108	21	USNM 394785	Yes
	BZE 7109*	34	USNM 394752	Yes
	BZE 7152	19	USNM 394346	Yes
	BZE 7232*	31	USNM 394762	Yes
	BZE 7350*	36	USNM 394753	Yes
	BZE 7671*	28	USNM 394786	Yes
	BZE 7672	24	USNM 394784	Yes
	BZE 7673*	22	USNM 394781	Yes
	BZE 7702	31	USNM 394783	Yes
	BZE 7703*	26	USNM 394782	Yes
	BZE 7726	24	USNM 394912	Yes
	BZE 7727	17	USNM 394911	Yes
	BZE 7735	23	USNM 394791	Yes
	CUR 8047	37	USNM 394886	Yes
	CUR 8048*	39	USNM 394884	Yes
	CUR 8049	33	USNM 394883	Yes
	CUR 8050*	38	USNM 394885	Yes
	CUR 8262*	24	USNM 394887	Yes
	CUR 8263	33	USNM 394888	Yes
	BAH 8046*	41	USNM 394903	Yes
	BAH 8047*	37	USNM 394902	Yes
	Navassa (no DNA)	3 (32–33)	USNM 360458	No
C. alloides	BZE 7233*	24	USNM 394754	Yes
	BZE 7264*	19	USNM 394755	Yes
	BZE 7761*	12	USNM 394910	Yes
	BZE (no DNA)	21	USNM 267843	No
	CUR 8325*	18	USNM 394882	Yes
C. kuna	BZE 4586*	6	No voucher	No
	BZE 5134*	7.5	No voucher	Yes
	BZE 6049*	7	No voucher	Yes
	BZE 6387*	7.5	No voucher	Yes
	PAN; holotype* DNA from GenBank	17.1	SIO-07-5	No
C. punctipectophorus	FLA; paratype (no DNA)	28	USNM 179307	No
	South Carolina (no DNA)	28	USNM 315530	No

[a] USNM = U.S. National Museum (National Museum of Natural History), Smithsonian Institution; AMNH = American Museum of Natural History; MOBR = Museo Oceanológico Hermano Benigno Román, Venezuela; SIO = Scripps Institution of Oceanography.