



# Two new species of the deepwater cardinalfish genus *Epigonus* (Epigonidae) from deep reefs off Curaçao, southern Caribbean

Makoto Okamoto<sup>1</sup> · Carole C. Baldwin<sup>2</sup> · Douglas J. Long<sup>3</sup>

Received: 20 September 2023 / Revised: 24 December 2023 / Accepted: 9 January 2024 / Published online: 28 February 2024  
© The Author(s) under exclusive licence to The Ichthyological Society of Japan 2024

## Abstract

Two new species of deepwater cardinalfish, *Epigonus gemma* [7 specimens, 37.7–76.7 mm in standard length (SL)] and *Epigonus hexacanthus* (22 specimens, 32.2–57.0 mm SL) are described based on specimens from deep reefs off Curaçao, southern Caribbean Sea. *Epigonus gemma* is distinguished from other congeners by a combination of the following characters: dorsal-fin rays VII-I, 9–10; pectoral-fin rays 16; total gill rakers 25–27; vertebrae 10 + 15; pyloric caeca 8–9; pored lateral-line scales 43–44 + 5–6; opercular spine absent; maxillary mustache-like processes absent; ribs on last abdominal vertebra absent; tongue toothless; endopterygoid teeth absent; and enlarged conical teeth on symphysis of lower jaw present. *Epigonus hexacanthus* is distinguished from other congeners by a combination of the following characters: dorsal-fin rays VI-I, 10; pectoral-fin rays 16–17; total gill rakers 25–27; vertebrae 10 + 15; pyloric caeca 6–7; pored lateral-line scales 32–35 + 3–5; opercular spine absent; maxillary mustache-like processes absent; ribs on last abdominal vertebra absent; lingual teeth present; endopterygoid teeth present; and enlarged conical teeth on symphysis of lower jaw absent. Eight specimens (37.6–54.4 mm SL) of *E. hexacanthus* are female with mature gonads, rendering the species the smallest in size at sexual maturity among its congeners. A key to the species of *Epigonus* currently known from the Caribbean Sea is provided.

**Keywords** Submersible · COI · Curaçao · Deep Reef Observation Project (DROP)

## Introduction

The deepwater cardinalfish genus *Epigonus* Rafinesque 1810 is the most species-rich and widely distributed genus in the family Epigonidae, with 40 valid species (Mayer 1974;

Abramov 1992; Okamoto and Miyamoto 2022). In several taxonomic studies of *Epigonus*, the first author proposed four species groups (Okamoto 2011, 2012; Okamoto and Motomura 2011, 2013): the *Epigonus constanciae* group, the *Epigonus oligolepis* group, the *Epigonus pandionis* group, and the *Epigonus telescopus* group. Recent taxonomic studies of the genus have focused on the Indo-Pacific region (Okamoto 2018; Okamoto and Gon 2018; Okamoto et al. 2020; Okamoto and Miyamoto 2022), and study in the western Atlantic Ocean has not progressed since Mayer (1974). Previous submersible diving off Curaçao in the southern Caribbean as part of the Smithsonian's Deep Reef Observation Project (DROP) collected two species of *Epigonus* that are morphologically distinct from currently known species. These species are described herein, and a key to the species in the Caribbean Sea is provided.

## Materials and methods

Specimens were collected on dives made in 2012–2014 in the human-occupied submersible *Curasub* (<http://www.substation-Curacao.com>). Fish specimens were collected

---

This article was registered in the *Official Register of Zoological Nomenclature* (ZooBank) as 440A7C80-84A3-490D-A33A-27B6E B7D79CF.

This article was published as an Online First article on the online publication date shown on this page. The article should be cited by using the doi number.

---

✉ Makoto Okamoto  
epigonidae@gmail.com

<sup>1</sup> Marine Fisheries Research and Development Center, Japan Fisheries Research and Education Agency, 6F Techno Wave 100, 1-1-25 Shin-urashima-cho, Kanagawa-ku, Yokohama, Kanagawa 221-5829, Japan

<sup>2</sup> Department of Vertebrae Zoology, National Museum of Natural History, Smithsonian Institution, 20560, Washington D.C., USA

<sup>3</sup> Department of Ichthyology, California Academy of Sciences, 55 Music Concourse Dr., San Francisco, CA 94118, USA

using the fish anesthetic quinaldine pumped from a reservoir through a tube attached to one hydraulic arm of the sub and a suction hose attached to the other arm. The hose empties into a vented plexiglass cylinder attached to the outside of the sub. At the surface, some specimens were measured, photographed, tissue sampled (muscle biopsy from right side) and preserved.

Meristic and morphometric methods followed Mayer (1974) and Okamoto (2011). Missing lateral-line scales were estimated by counting scale pockets. The number of pored lateral-line scales on the caudal fin is represented as “+  $n$ ”. The first caudal vertebra is defined as the first vertebra bearing a definite hemal spine. Measurements were made with calipers to the nearest 0.1 mm. Terminology and formula of the supraneural bones follows Mabee (1988) and Ahlstrom et al. (1976), respectively. Counts of supraneurals, vertebrae, and ribs were taken from radiographs. The term “maxillary mustache-like process” is used for a process on the maxillary head (see Okamoto 2011: fig. 3). The number of pyloric caeca and sex were established by dissection of the abdomen on the right side. Standard length is abbreviated as SL. Institutional codes follow Sabaj (2020).

Tissue samples for DNA Barcoding were stored in saturated salt-DMSO (dimethyl sulfoxide) buffer (Seutin et al. 1991). DNA extraction, PCR, sequencing cytochrome c oxidase subunit I (COI), and editing COI sequences were performed as outlined by Weigt et al. (2012). Sequences were uploaded to the Barcode of Life Database (Bin Numbers BOLD: ACG7476 and BOLD: ACG7477, boldsystems.org) and Genbank (Accession numbers OR918549–OR918570), and sequences of the holotypes of the two species were entered into the BOLD search engine for comparison with other available sequences of *Epigonus*.

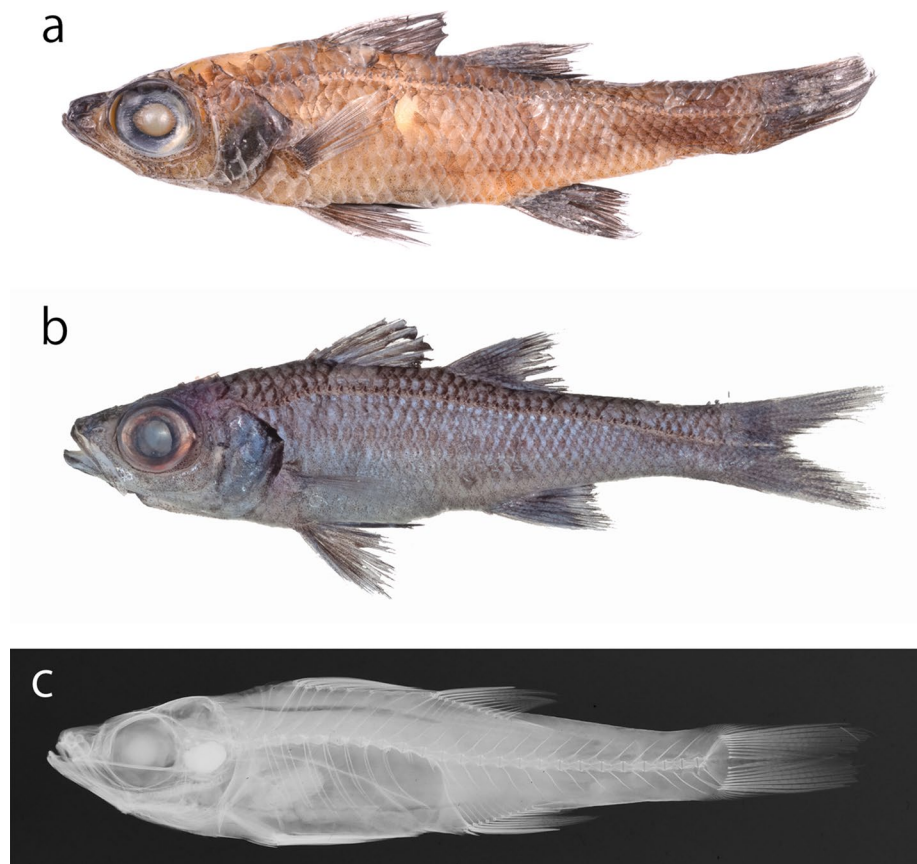
### *Epigonus gemma* sp. nov.

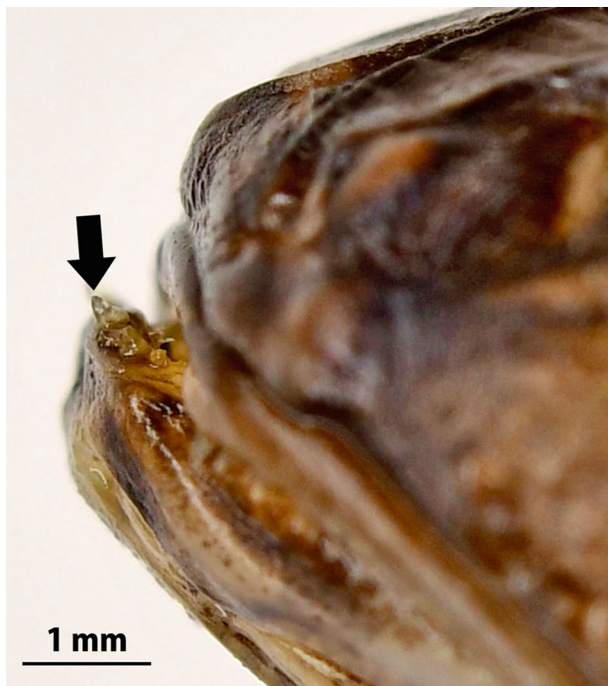
(Figs. 1, 2)

**Holotype.** USNM 431654, 76.7 mm SL, male, DNA #CUR14082, *Curasub* submersible, sta. 14-12, Curaçao, east of downline at Substation Curaçao, 12°05.00'N, 68°53.57'W, 275 m depth, 16 September 2014, C. Baldwin, L. Weigt, B. Van Bebber, R. Betancur.

**Paratypes.** 6 specimens: USNM 413854, 71.5 mm SL, male, DNA #CUR12009, *Curasub* submersible, sta. 12-01,

**Fig. 1** *Epigonus gemma* sp. nov. **a** USNM 431654, holotype, 76.7 mm SL, preserved specimen; **b** USNM 413854, paratype, 71.5 mm SL, fresh specimen (photographed by C. C. Baldwin); **c** USNM 413858, paratype, 62.6 mm SL, radiograph





**Fig. 2** Lateral view of mouth of *Epigonus gemma* sp. nov., USNM 413854, paratype, 71.5 mm SL. Arrow shows enlarged conical teeth on symphysis of lower jaw

Curaçao, off Substation Curaçao downline, 12°04.59'N, 68°53.56'W, 171–309 m depth, 21 May 2012, C. Baldwin, A. Schrier, B. Brandt; USNM 413858, 62.6 mm SL, male, DNA #CUR12088, USNM 413859, 54.7 mm SL, sex unknown, DNA #CUR12089, USNM 413861, sex unknown, DNA #CUR12091, *Curasub* submersible, sta. 12-12, Curaçao, east of downline at Substation Curaçao, 12°04.59'N, 68°53.56'W, 156–290 m depth, 7 August 2012, C. Baldwin, A. Schrier, D. Pawson; USNM 413862, 53.5 mm SL, sex unknown, DNA #CUR12296, *Curasub* submersible, sta. 12-18, Curaçao, off Substation Curaçao downline, 12°04.59'N, 68°53.56'W, 291–294 m depth, 14 August 2012, A. Schrier, B. Brandt, C. Baldwin, A. Driskell; USNM 431690, 76.1 mm SL, male, DNA #CUR14082, *Curasub* submersible, sta. 14-09, Curaçao, east of downline at Substation Curaçao, 12°04.59'N, 68°53.56'W, 265–293 m depth, 24 June 2014, C. Baldwin, B. Brandt, A. Schrier.

**Diagnosis.** A species of *Epigonus* with the following combination of characters: dorsal-fin rays VII-I, 9–10; pectoral-fin rays 16; total gill rakers 25–27; vertebrae 10 + 15; pyloric caeca 8–9; pored lateral-line scales 43–44 + 5–6; opercular spine absent; maxillary mustache-like processes absent; ribs on last abdominal vertebra absent; tongue toothless; endopterygoid teeth absent; enlarged conical teeth on symphysis of lower jaw present.

The DNA barcode for the holotype (USNM 431654) is as follows: NNNNNNNNNNNNNNNNNNNNNNNNNNNNNCCTTTA

TCTCGTATTTGGTGCTTGAGCCGGAATAGTGGGCAC  
AGCCTTAAGCCTGCTTATTCGGGCAGAACTCAGCCA  
ACCAGGCGCCCTCCTCGGAGACGACCAGATCTATAA  
CGTAATTGTTACAGCACACGCCTTCGTAATAATTTT  
CTTTATAGTAATACCAATTATGATTGGGGGCTTCGG  
AAATTGGCTTATCCCTTTAATAATTGGGGCCCCTGA  
TATAGCCTTCCCTCGAATAAATAATATAAGCTTTTG  
ACTCCTCCCTCCTTCCCTCCTGCTCCTTCTTGCCCTC  
TTCTGGGGTAGAAGCCGGTGCCGGCACCGGCTG  
AACAGTTTACCCCTCTGGCTGGGAACCTTAGCCCA  
CGCGGGGGCCTCTGTTGATTTAACAATCTTTTCTCT  
ACATCTTGCAAGTATTTCTCAATTCTTGGGGCTAT  
TAACTTTATTACAACAATTATTAATATAAAACCCCC  
GGCCATTTACAATAACCAAACACCCCTGTTTGTGTG  
AGCAGTATTAATTACCGCAGTTCTTCTTCTGCTGTC  
CCTCCCTGTCCTTGCTGCTGGAATTACAATGCTTCT  
TACAGACCGAAACCTCAACACCACCTTCTTTGACCC  
GGCAGGAGGAGGGGACCCCATCCTCTACCAACA  
CCTGTTNNNNNNNNNN.

**Description.** Counts and proportional measurements are given in Table 1. Data for the holotype are presented first, followed by data of paratypes (if different) in parentheses. Body moderately slender, laterally compressed, nape slightly humped, deepest at pectoral-fin base (Fig. 1). Head large, laterally compressed. Maxillary mustache-like process absent. Snout short and round; two nostrils close-set without dermal flap, anterior nostril short and with membranous tube, posterior nostril elliptical. Eye large, round, diameter slightly shorter than postorbital length (subequal); bony rim of orbit slightly raised above dorsal profile; interorbital region flat. Mouth large, terminal, gape oblique; posterior margin of maxilla extending to below anterior margin of pupil; lower jaw slightly projecting when mouth closed; nob-like structures absent on symphysis of lower jaw. Upper jaw teeth small conical, arranged in a single series visible when mouth closed. Lower jaw teeth small conical, arranged in a single series; tip of lower jaw curved slightly upward, symphysis forming a thick bony projection, three enlarged conical teeth on each side of symphysis of lower jaw (one to three enlarged conical teeth on each side of symphysis of lower jaw; Fig. 2). Small number of villiform teeth present on vomer. Single row of small conical teeth (rarely two rows) on palatines. Tongue and endopterygoid toothless. Opercular spine absent; preopercle without spines, ventral and posterior margins smooth. Origin of first-dorsal fin located behind base of pelvic fin; first dorsal-fin spine minute; fourth dorsal-fin spine the longest, length longer than orbital diameter; two supernumerary spines on first dorsal pterygiophore. Spine of second dorsal fin long. First and second dorsal fins separated by gap longer than snout length. Origin of anal fin vertically below 4th soft ray of second dorsal-fin; first anal-fin spine minute; second spine long, length longer than orbital diameter; two supernumerary spines on first anal

**Table 1** Counts and measurements of *Epigonus gemma* sp. nov. and *Epigonus hexacanthus* sp. nov.

	<i>Epigonus gemma</i>		<i>Epigonus hexacanthus</i>	
	Holotype USNM 431654	Paratypes (n = 6)	Holotype USNM 422678	Paratypes (n = 11)
Standard length (mm)	76.7	37.7–76.1	54.4	33.0–56.3
Counts				
Dorsal-fin rays	VII-I, 10	VII-I, 9–10	VI-I, 10	VI-I, 10
Anal-fin rays	II, 9	II, 9	II, 9	II, 9
Pectoral-fin rays	16	16	16	16–17
Pored lateral-line scales	43 + 5	43–44 + 5–6	34 + 5	32–35 + 3–5
Scales above lateral line	2	2	2	2
Scales below lateral line	9	8–9	7	7
Gill rakers	7 + 19 = 26	6–7 + 19–20 = 25–27	6 + 20 = 26	6 + 19–21 = 25–27
Pyloric caeca	8	9	7	6–7
Vertebrae	10 + 15	10 + 15	10 + 15	10 + 15
Measurements (% standard length)				
Head length	32.7	31.0–34.6	33.8	33.6–39.4
Head width	14.9	11.1–14.8	14.2	13.4–17.6
Head height	16.2	14.8–17.3	14.7	13.0–17.6
Body depth	22.8	21.4–25.0	19.3	18.6–21.9
Body width	13.8	9.3–14.1	12.5	11.4–14.7
Caudal-peduncle depth	10.3	8.6–10.6	8.8	8.1–9.8
Caudal-peduncle length	29.6	26.7–29.6	27.4	26.9–30.7
Orbital diameter	12.3	12.0–12.7	12.3	11.8–14.5
Interorbital width	7.6	6.4–7.3	8.1	7.8–9.8
Postorbital length	12.5	10.8–13.9	12.7	10.7–14.2
Upper-jaw length	14.1	12.6–14.9	15.1	14.5–16.8
Lower-jaw length	15.3	14.1–17.2	15.6	15.5–18.2
Snout length	6.9	6.8–9.0	9.2	8.2–9.9
Pre-1st dorsal-fin length	37.3	35.8–41.1	39.0	35.9–43.3
Pre-2nd dorsal-fin length	57.6	56.1–60.4	54.2	53.3–61.7
Pre-pectoral-fin length	32.1	31.7–36.9	33.8	34.3–39.3
Pre-pelvic-fin length	35.6	35.5–39.5	36.8	36.9–41.2
Pre-anus length	57.2	54.3–60.7	55.5	54.2–64.5
Pre-anal-fin length	64.5	61.7–66.5	62.9	59.9–68.1
1st spine length on 1st dorsal-fin	2.9	2.6–3.5	9.6	9.4–13.1
2nd spine length on 1st dorsal-fin	15.5	12.5–15.1	10.1	11.9–15.9
3rd spine length on 1st dorsal-fin	16.4	14.3–16.3	11.6	12.6–15.6
2nd dorsal-fin spine length	14.1	11.4–13.5	8.8	8.9–13.9
1st anal-fin spine length	2.0	1.5–2.2	1.5	1.2–1.9
2nd anal-fin spine length	15.1	10.6–14.5	7.4	7.8–11.3
Pelvic-fin spine length	14.9	11.4–15.4	9.0	8.2–11.5
1st dorsal-fin base	11.6	10.8–12.6	10.5	8.9–11.4
2nd dorsal-fin base	10.6	10.5–12.8	9.9	9.1–10.6
Anal-fin base	10.0	9.3–11.3	8.8	8.2–9.6
Pectoral-fin length	18.1	17.2–20.7	19.9	19.0–23.4
Pelvic-fin length	21.5	17.7–21.7	14.3	14.7–18.0

pterygiophore. Pectoral fin short, posterior tip of fin not reaching to vertical line from anus. Pelvic fin long, posterior tip just before to anus. Caudal fin deeply forked. Anus located vertically below origin of second dorsal-fin base. Ribs absent on last abdominal vertebra (Fig. 1c). Supraneural bones 3 (0+0/0+2/1+1/1). Scales deciduous, small, weakly ctenoid, covering the whole body except snout tip, anterior to rim of orbit, and surface of jaws; scales also present on bases of second dorsal, anal and caudal fins; series of pored lateral-line scales complete, 5 (5–6) pored scales on caudal fin. No trace of luminous organ around belly or pyloric caeca.

**Color when fresh** (Fig. 1b). Dorsal portions of body and head light purple; ventral surface and lower half of body silvery-tan. All fins light black. Gill cover light blue, posterior margin black.

**Color in alcohol** (Fig. 1a). Body and head uniformly light brown, except for the snout and gill cover which are dark gray. Dorsal, anal, pelvic, and caudal fins dark gray, with many melanophores on the soft rays and membranes. Pectoral fin light gray except for dark base. Mouth cavity tan.

**Distribution.** Known only from Curaçao, southern Caribbean.

**Habitat.** Epigonids are common at Curaçao at depths near the lower limit of the *Curasub* (300 m), especially in caves and crevices along a near-vertical rock wall [Electronic Supplementary Material (ESM) Video S1]. All specimens described in this study, including those of *E. gemma* sp. nov., were collected in this habitat.

**Etymology.** The specific name *gemma* is from the Latin meaning bud, in reference to the enlarged conical teeth on each side of the symphysis of the lower jaw (Fig. 2).

**Comparison.** *Epigonus gemma* sp. nov. belongs to a group of similar species in the *E. pandionis* group (Okamoto and Motomura 2013). The *E. pandionis* group is distinguished from the other three species groups of the genus (the *E. constanciae* group, *E. oligolepis* group, and *E. telescopus* group) in having more than 43 pored lateral-line scales, lacking an opercular spine, and having VII–I, 9–11 dorsal-fin rays (Okamoto and Motomura 2013). Okamoto and Motomura (2013) indicated that the *E. pandionis* group comprises nine species, viz., *Epigonus cavaticus* Ida et al. 2007; *Epigonus denticulatus* Dieuzeide 1950; *Epigonus elongatus* Parin and Abramov 1986; *Epigonus fragilis* (Jordan and Jordan 1922); *Epigonus lifouensis* Okamoto and Motomura 2013; *Epigonus marisrubri* Krupp et al. 2009; *Epigonus pandionis* (Goode and Bean 1881); *Epigonus parini* Abramov 1987; and *Epigonus tuberculatus* Okamoto and Motomura 2013. *Epigonus gemma* sp. nov. is unique in the group in having enlarged conical teeth on each side of the symphysis of lower jaw (vs. absent).

In addition, *E. gemma* sp. nov. can be distinguished from *E. denticulatus*, *E. elongatus*, *E. lifouensis*, *E. marisrubri*,

*E. pandionis*, *E. parini*, and *E. tuberculatus* by having 16 pectoral-fin rays and 25–27 gill rakers (vs. 18–21 and 28–34, respectively in *E. denticulatus*; 18–20 and 28–34 in *E. elongatus*; 18–19 and 24–25 in *E. lifouensis*; 17–18 and 29–30 in *E. marisrubri*; 17–19 and 26–30 in *E. pandionis*; 18–20 and 35–39 in *E. parini*; and 19–20 and 21–22 in *E. tuberculatus*; Okamoto and Motomura 2013, table 2). *Epigonus cavaticus* and *E. fragilis* are similar to *E. gemma* sp. nov. in having overlapping pectoral-fin rays and gill rakers but differ from *E. gemma* sp. nov. in having a large number of pored lateral-line scales (48–50 in *E. cavaticus* and 46–49 in *E. fragilis* vs. 43–44 in *E. gemma* sp. nov.) and a pair of ribs on the last abdominal vertebra (vs. absent in *E. gemma* sp. nov.; Fig. 1c). *Epigonus gemma* sp. nov. is distinguished from the second new species in the present study, *Epigonus hexacanthus* sp. nov., in having enlarged conical teeth on symphysis of lower jaw (vs. absent in *E. hexacanthus*), 7 spines on the first dorsal-fin (vs. 6 spines), and 43–44 lateral-line scales (vs. 32–35 lateral-line scales).

**Remarks.** Within *Epigonus*, only *Epigonus exodon* Okamoto and Motomura 2012 and *Epigonus glossodontus* Gon 1985 have the enlarged conical teeth on each side of the lower-jaw symphysis present in *E. gemma* (Okamoto and Gon 2018; Okamoto et al. 2020). *Epigonus exodon* has been reported to undergo growth changes in those teeth (Okamoto and Motomura 2012), but no growth changes in those teeth were found in *E. gemma* sp. nov. between 37.3 mm SL and 76.7 mm SL.

The holotype and seven paratypes of *E. gemma* sp. nov. are males of 62.6–76.7 mm SL with a large testis. The sex of the remaining type specimens was unknown. Although no mature eggs were found, the present species is most likely a small species.

The DNA barcode of the holotype, USNM 431654, clusters in BOLD with six other sequences of *E. gemma* sp. nov. from Curaçao (USNM 413854, 413858, 413859, 413861, 413862, 431690). That lineage is approximately 5% divergent from “*Epigonus* sp.” from India (accession number: GBMND26919–21, GBMND26920–21, and GBMND26921–21) and 11% divergent from *Epigonus hexacanthus* sp. nov. From other species of *Epigonus* known from the Caribbean Sea that are represented in the BOLD database [*E. denticulatus*, *Epigonus macrops* (Brauer 1906), *E. pandionis*], the barcode of *E. gemma* differs by more than 17%. Intraspecific divergence in COI sequences for *E. gemma* is <0.5%.

### ***Epigonus hexacanthus* sp. nov.**

(Figs. 3, 4)

**Fig. 3** *Epigonus hexacanthus* sp. nov. **a** USNM 422678, holotype, 54.4 mm SL, preserved specimen; **b** USNM 413950, paratype, 44.1 mm SL, fresh specimen (photographed by C. C. Baldwin); **c** USNM 431760, paratype, 56.3 mm SL, radiograph



**Fig. 4** *In situ* image of *Epigonus hexacanthus* sp. nov. taken by the submersible *Curasub* on 23 May 2013, at 265 m near the bottom of rock wall at Curaçao (photographed by C. C. Baldwin and D. R. Robertson)



**Holotype.** USNM 422678, 54.4 mm SL, female, DNA #CUR13115, *Curasub* submersible, sta. 13-06, Curaçao, east of downline at Substation Curaçao, 12°04.59'N, 68°53.56'W, 265 m depth, 23 May 2013, D. Robertson, M. Harasewych, C. Castillo, B. Brandt.

**Paratypes.** 11 specimens: USNM 413950, 44.1 mm SL, female, DNA # CUR13064, USNM 413951, 42.8 mm SL, male, *Curasub* submersible, sta. 13-01, Curaçao, off Substation Curaçao downline, 12°04.59'N, 68°53.56'W, 52–304 m depth, 5 February 2013, C. Baldwin, L. Weigt, L.

Wacchaus, B. Brandt, J. Piraino; USNM 426792, 33.3 mm SL, sex unknown, DNA #CUR13295, *Curasub* submersible, sta. 13-21, Curaçao, off Substation Curaçao downline, 12°04.59'N, 68°53.56'W, 247 m depth, 17 August 2013, C. Baldwin, A. Schrier, B. Brandt, A. Driskell; USNM 431707, 50.1 mm SL, female, DNA #CUR14099, *Curasub* submersible, sta. 14-12, Curaçao, east of downline at Substation Curaçao, 12°05.00'N, 68°53.57'W, 265 m depth, 16 September 2014, C. Baldwin, L. Weigt, B. Van Bebber, R. Betancur; USNM 431760, 7 specimens, 56.3 mm SL, female, 47.4 mm SL, female, 47.0 mm SL, female, 44.0 mm SL, female, 37.6 mm SL, female, 35.8 mm SL, male, 32.3 mm SL, male, *Curasub* submersible, sta. 14-12, Curaçao, east of downline at Substation Curaçao, 12°05.00'N, 68°53.57'W, 275 m depth, 16 September 2014, C. Baldwin, L. Weigt, B. Van Bebber, R. Betancur.

**Non-type specimens.** 10 specimens (all specimens were subjected to DNA analysis). USNM 413848 (44.0 mm SL, DNA #CUR12003), USNM 413849 (46.0 mm SL, DNA #CUR12004), USNM 413850 (49.0 mm SL, DNA #CUR12005), USNM 413851 (35.0 mm SL, DNA #CUR12006), USNM 413852 (37.0 mm SL, DNA #CUR12007), USNM 413853 (33.0 mm SL, DNA #CUR12008), USNM 413855 (34.0 mm SL, DNA #CUR12014), USNM 413857 (40.0 mm SL, DNA #CUR12016), *Curasub* submersible, sta. 12-01, Curaçao, off Substation Curaçao downline, 12°04.59'N, 68°53.56'W, 171–309 m depth, 21 May 2012, C. Baldwin, A. Schrier, B. Brandt; USNM 413860, 50.0 mm SL, DNA #CUR12090, *Curasub* submersible, sta. 12-12, Curaçao, east of downline at Substation Curaçao, 12°04.59'N, 68°53.56'W, 156–290 m depth, 7 August 2012, C. Baldwin, A. Schrier, D. Pawson; USNM 431705, 57.0 mm SL, DNA #CUR14097, *Curasub* submersible, sta. 14-12, Curaçao, off Substation Curaçao downline, 12°05.00'N, 68°53.57'W, 174–297 m depth, 16 September 2014, C. Baldwin, L. Weigt, B. Van Bebber, R. Betancur.

**Diagnosis.** A species of *Epigonus* with the following combination of characters: dorsal-fin rays VI-I, 10; pectoral-fin rays 16–17; total gill rakers 25–27; vertebrae 10 + 15; pyloric caeca 6–7; pored lateral-line scales 32–35 + 3–5; opercular spine absent; maxillary mustache-like processes absent; ribs on last abdominal vertebra absent; lingual teeth present; endopterygoid teeth present; enlarged conical teeth on symphysis of lower jaw absent.

The DNA barcode for the holotype (USNM 422678) is as follows: NNNNNNNNNNNNNNNNNNNNNNNNNNNCCTCTA TCTAGTATTTGGTGCTTGAGCTGGAATAGTAGGCAC AGCCTTGAGTCTGCTTATTCGGGCAGAACTCAGCCA ACCCGGCGCCCTCCTTGAGACGACCAGATCTATAA CGTAATTGTTACGGCGCATGCTTTCGTAATAATTT CTTTATAGTAATACCAATCATAATTGGGGGTTTCGG AAATTGACTTATCCCTTAATAATCGGGGCTCCTGA

TATGGCCTTCCCTCGTATAAACAACATAAGCTTTTG ACTCCTCCCTCCTTCTTCTACTCCTCCTTGCCCTC TTCTGGGGTAGAAGCAGGAGCCGGCACTGGGGTG AACTGTCTACCCCCCTTTAGCTGGTAATCTCGCCCA CGCGGGAGCCTCTGTTGACTTAACAATCTTTTCCCT ACATTTAGCAGGTATTTCTCAATTCTTGGGGCCAT TAACTTCATTACAACAATTATTAACATAAAAACCTCC TGCCATCTCTCAATATCAAACACCTTTATTTGTGTG GGCAGTCTTAATTACAGCAGTCCTTCTTCTACTTTC TCTCCCCGTACTTGCTGCTGGAATTACAATGCTCCT TACGGACCGAAATCTTAACACCCTTTCTTTGACCC AGCAGGGGGAGGGGATCCCATCCTTTATCAACACCT GTTTNNNNNNNNNN.

**Description.** Counts and proportional measurements are given in Table 1. Data for the holotype are presented first, followed by data of paratypes (if different) in parentheses. Body slender, laterally compressed, nape not humped, deepest at pectoral-fin base (Fig. 3). Head large, laterally compressed. Maxillary mustache-like process absent. Snout short and round; two nostrils close-set without dermal flap, anterior nostril short and with membranous tube, posterior nostril elliptical. Eye large, round, diameter subequal to postorbital length; bony rim of orbit slightly raised above dorsal profile; interorbital region concave at center. Mouth large, terminal, gape oblique; posterior margin of maxilla extending to below anterior margin of pupil; lower jaw not projecting when mouth closed; nob-like structures absent on symphysis of lower jaw. Upper jaw teeth minute, arranged in a single series, widely space. Lower jaw teeth minute, arranged in a single series, except two rows at symphysis of lower jaw, no enlarged teeth near symphysis. Vomerine teeth minute, small number of teeth scattered on anterior part and extending posteriorly along midline of palate. Palatine teeth minute, single row. Endopterygoids bearing single row of small conical teeth. Lingual teeth minute, arranged around outer edge of tongue and two rows near center, not forming dense tooth patch. Opercular spine absent; preopercle without spines, ventral and posterior margins smooth. Origin of first-dorsal fin located behind base of pelvic fin; first dorsal-fin spine long; third dorsal-fin spine the longest, length shorter than orbital diameter; two supernumerary spines on first dorsal pterygiophore. Spine of second dorsal fin long. First and second dorsal fins separated by gap longer than snout length. Origin of anal fin vertically below posterior portion of second dorsal-fin base; first anal-fin spine minute; second spine long, length shorter than orbital diameter; two supernumerary spines on first anal pterygiophore. Pectoral fin long, posterior tip of fin just reaching to vertical line from anus. Pelvic fin short, posterior tip not reaching to anus. Caudal fin deeply forked. Anus located vertically below origin of second dorsal-fin base. Ribs absent on last abdominal vertebra (Fig. 3c). Supraneural bones 3 (/0+0/0+1/1+1/1/). Scales deciduous, large, weakly ctenoid, covering the whole

body except snout tip, anterior to rim of orbit, and surface of jaws; scales also present on bases of second dorsal, anal and caudal fins; series of pored lateral-line scales complete, 5 (3–5) pored scales on caudal fin. No trace of luminous organ around belly or pyloric caeca.

**Color when fresh** (Fig. 3b). Dorsal portion of body and head light gray; lower half of body silvery-white. Abdominal cavity semitransparent with inner black peritoneum. Pectoral, pelvic, and anal fins white. Dorsal and caudal fins light black.

**Color in alcohol** (Fig. 3a). Body and head uniformly light brown, except for abdominal cavity and gill cover which are beige. Pelvic fin white; pectoral, dorsal and caudal fins light brown, with many melanophores on the soft rays and membranes. Mouth cavity tan.

**Distribution.** Known only from Curaçao, southern Caribbean.

**Habitat.** Epigonids are common at Curaçao at depths near the lower limit of the *Curasub* (300 m), especially in caves and crevices along a near-vertical rock wall (Fig. 4; ESM Video S2). All specimens described in this study, including those of *E. hexacanthus*, were collected in this habitat.

**Etymology.** The specific name *hexacanthus* is derived from the Greek *hexa*-(six) and *acanthus* (spine) in reference to six spines on the first dorsal fin.

**Comparison.** *Epigonus hexacanthus* sp. nov. is unique in the genus in having six spines in the first dorsal-fin (vs. seven or eight spines in the first dorsal-fin; Okamoto and Gon 2018). Abramov (1987) described *E. parini* as having six spines in the first dorsal-fin, but Okamoto and Motomura (2013) noted that this species clearly has seven.

*Epigonus hexacanthus* sp. nov. belongs to the *E. oligolepis* group defined by Okamoto and Motomura (2011). The *E. oligolepis* group is distinguished from the other three species groups of the genus (the *E. constanciae* group, *E. pandionis* group, and *E. telescopus* group) in having 33–40 pored lateral-line scales (vs. 43–51 in the other three species groups; Okamoto and Motomura 2011; Okamoto and Gon 2018). Besides the present species, this species group comprises 6 species: *Epigonus carbonarius* Okamoto and Motomura 2011; *Epigonus devaneyi* Gon 1985; *E. exodon*; *E. glossodontus*; *Epigonus indicus* Idrees Babu and Akhilesh 2020; *Epigonus oligolepis* Mayer 1974. *Epigonus hexacanthus* sp. nov. can be distinguished from *E. devaneyi* and *E. indicus* by having lingual teeth (vs. absent; Okamoto and Motomura 2011; Idrees Babu and Akhilesh 2020). The present species also differs from *E. carbonarius* and *E. oligolepis* in having 25–27 gill rakers (vs. 21–23 in *E. carbonarius* and 29–32 in *E. oligolepis*). *Epigonus hexacanthus* sp. nov. differs from *E. exodon* and *E. glossodontus* by lacking enlarged conical teeth on the symphysis of lower jaw (vs. present; Gon 1985; Okamoto et al. 2020).

**Remarks.** Most species of *Epigonus* were described from adult specimens measuring 80–200 mm SL (Okamoto 2011, 2012, 2015; Okamoto and Motomura 2011, 2013; Okamoto and Gon 2018), and only *Epigonus angustifrons* Abramov and Manilo 1987 and *Epigonus telescopus* (Risso 1810) exceed 300 mm SL (Abramov 1992; Okamoto and Gon 2018). Ida et al. (2007) showed that *E. cavaticus* attains sexual maturity at the smallest size among the congeners, as females 63.7–66.8 mm SL had mature gonads. In this study, the holotype and seven paratypes of *E. hexacanthus* sp. nov. are females of 37.6–54.4 mm SL with a great number of eggs at several developmental stages. The most developed eggs were ca. 0.3 mm in diameter and were round with a single oil globule. Thus, *E. hexacanthus* sp. nov. seems to attain sexual maturity at the smallest size among the species.

The DNA barcode of the holotype, USNM 422678, clusters with 15 other sequences of *E. hexacanthus* from Curaçao in BOLD (USNM 413705, 413707, 413848, 413849, 413850, 413851, 413852, 413853, 413855, 413857, 413860, 426792, 413950, 413951, 433523). That lineage is approximately 11% divergent from *E. gemma*, 13% divergent from “*Epigonus* sp.” from India (GBMND26919–21, GBMND26920–21, and GBMND26921–21). From other species of *Epigonus* known from the Caribbean Sea that are represented in the BOLD database (*E. denticulatus*, *E. macrops*, *E. pandionis*), the barcode of *E. hexacanthus* differs by more than 19%. Intraspecific divergence in COI sequences for *E. hexacanthus* is < 1%.

*Epigonus indicus* Idrees Babu and Akhilesh 2020, which is in the same species group as *E. hexacanthus* sp. nov., was described as having 10 + 14 vertebrae, a count they considered as an important diagnostic character for the species. However, the radiograph in Idrees Babu and Akhilesh (2020, fig. 3) reveals a vertebral count of 10 + 15. Fishes of the genus *Epigonus* have total of 25 vertebrae, with abdominal and caudal vertebral counts of 10 + 15 or 11 + 14 (Mayer 1974; Okamoto and Gon 2018). Furthermore, Idrees Babu and Akhilesh (2020) suggested the presence of a ventral luminous organ based on a region of ventral fluorescent blue color in *E. indicus*. However, this is the peritoneum, not a ventral luminous organ. Among the species of the genus, only *E. macrops* has a ventral luminous organ, formed by a modification of one of eight pyloric caeca (Mayer 1974; Okamoto et al. 2012; Okamoto and Gon 2018).

## Key to species of *Epigonus* of the Caribbean Sea

In the taxonomic study of *Epigonus*, Mayer (1974) reported six species from the Caribbean Sea: *E. denticulatus*; *E. macrops*; *Epigonus occidentalis* Goode and Bean 1896; *E. oligolepis*; *Epigonus pectinifer* Mayer 1974; and *E.*



*pandionis*. Since then, Abramov (1992) and Gon (2003) have reported on the distribution of species of *Epigonus* in this area; however, no additional species have been found in the area. We provide a key to the species from the Caribbean Sea including the two species in this study.

- 1a. First dorsal-fin spines 6 ..... *E. hexacanthus*  
 1b. First dorsal-fin spines 7 ..... 2  
 2a. Pored lateral-line scales 33–36 ..... *E. oligolepis*  
 2b. Pored lateral-line scales more than 43 ..... 3  
 3a. Opercular spine present ..... 4  
 3b. Opercular spine absent ..... 5  
 4a. Tooth patch present on tongue; maxillary mustache-like processes pointed; gill rakers 26–30 ... *E. pectinifer*  
 4b. Tongue toothless; maxillary mustache-like processes absent; gill rakers 24–26 ..... *E. occidentalis*  
 5a. Gill rakers 18–20; ventral luminous organ present ..... *E. macrops*  
 5b. Gill rakers 25–34; ventral luminous organ absent ..... 6  
 6a. Enlarged teeth present on symphysis of lower jaw; pyloric caeca 8–9; ribs absent on last abdominal vertebra ..... *E. gemma*  
 6b. Enlarged teeth absent on symphysis of lower jaw; pyloric caeca 10–14; ribs present on last abdominal vertebra ..... 7  
 7a. Body moderately deep, body depth 22.4–29.6% SL; caudal-peduncle length 22.0–26.3% SL; gill rakers 26–30; 100–130 mm SL specimens with posterodorsally canted ring encircling the caudal peduncle (Mayer 1974; Okamoto and Motomura 2013) ..... *E. pandionis*  
 7b. Body slender, body depth 15.8–23.6% SL; caudal-peduncle length 25.9–33.1% SL; gill rakers 28–34; 100–130 mm SL specimens without posterodorsally canted ring on caudal peduncle ..... *E. denticulatus*

**Comparative materials.** *Epigonus denticulatus*: AMS I.21669-005, 2 specimens, 124.0–132.3 mm SL, 33°31'S, 152°04'E, New South Wales, Australia, 28 September 1977; AMS I.29540-002, 125.3 mm SL, 35°32'S, 150°46'E, New South Wales, Australia, 10 August 1977. *Epigonus exodon*: NTUM 13370, 131.0 mm SL, 13°03'S, 45°01'E, south of Mayotte, western South Indian Ocean, 504 m depth, 27 January 2017. *Epigonus carbonarius*: holotype, MNHN 2010-983, 95.3 mm SL, female, 08°58'S, 140°04'W, off Nuku Hiva Island, Marquesas Islands, 391–408 m depth, 24 August 1997. *Epigonus macrops*: AMS I.22814-018, 131.6 mm SL, northwest of Port Headland, Western Australia, Indian Ocean, 704 m depth, 6 April 1982; AMS I.31161-004, 170.5 mm SL, off Cape Cuvier, Western Australia, Indian Ocean, 901 m depth, 28 January 1991. *Epigonus occidentalis*: UF 109570, 3 specimens, 69.8–88.2 mm SL, 24°14.1'N, 82°23.7'W, Florida Keys,

534 m depth, 8 June 1994; UF 113906, 2 specimens, 68.2–80.0 mm SL, 24°12.3'N, 82°37.5'W, Florida Keys, 559–577 m depth, 16 June 1998; UF 180268, 67.0 mm SL, 24°20.5'N, 83°14.5'W, Florida Keys, 144–157 m depth, 23 April 2003; UF 211404, 15 specimens, 60.3–92.9 mm SL, 14°23.0'N, 81°45.0'W, Caribbean Sea, 5 June 1962; UF 229213, 12 specimens, 61.2–187.5 mm SL, 14°35.0'N, 81°32.0'W, Caribbean Sea, 450–576 m depth, 31 January 1971. *Epigonus oligolepis*: UF 43252, 6 specimens, 104.5–150.3 mm SL, 26°11'N, 84°43'W, Gulf of Mexico, Florida, 300 m depth, 19 September 1985. *Epigonus pandionis*: UF 221291, 4 specimens, 136.7–182.0 mm SL, 03°45'N, 08°03'E, Equatorial Guinea, western Atlantic, 409–485 m depth, 14 May 1965; UF 221434, 19 specimens, 51.2–61.3 mm SL, 03°49'N, 07°38'E, Equatorial Guinea, western Atlantic, 264–269 m depth, 14 May 1965; UF 222947, 3 specimens, 162.9–180.0 mm SL, Caribbean Sea, 373–434 m depth, 14 July 1966. *Epigonus pectinifer*: HUMZ 190275, 67.1 mm SL, 08°10'3"S, 109°49'3"E–08°09'4"S, 109°48'8"E, off Java, Indonesia, 280–285 m depth, 13 September 2004.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10228-024-00948-2>.

**Acknowledgments** We are most grateful to the following persons and institutions for specimen loans: M. McGrouther, A. Hay, and S. Reader (AMS); M. Yabe, H. Imamura, F. Tashiro, and T. Kawai (HUMZ); P. Pruvost and R. Causse (MNHN); J. Williams, E. Wilbur, D. Pitassy, and K. Murphy (USNM), W.-J. Chen, M.-Y. Lee, H.-S. Lin, and J.-N. Chen (NTUM); L. M. Page, R. H. Robins and R. A. Singer (UF). We also thank M. Matsunuma (Kyoto University Museum), G. Shinohara and K. Fujiwara (National Museum of Nature and Science, Tsukuba) for taking x-rays. B. Brandt, B. Brown, T. Christiaan, L. Schenk, A. “Dutch” Schrier, and B. van Bebbler assisted in various ways with submersible operations; C. Castillo and T. Devine provided project management and DNA technician services for DROP. M. Girard for capturing and editing video. This is Ocean Heritage Foundation/Curaçao Sea Aquarium/Substation Curaçao (OHF/SCA/SC) contribution number OHF/SCA/SC#55.

## Declarations

**Conflicts of interest** This paper has no conflict of interest.

**Ethics approval** Fish species, treated in this study, are not listed as threatened or endangered by the IUCN Red List or CITES. Specimens registered in fish collections of natural history museum were used in this study.

## References

- Abramov AA (1987) A new *Epigonus* species (Perciformes, Epigonidae) from the southern Pacific. *Vopr Ikhtiol* 27:1010–1013  
 Abramov AA (1992) Species composition and distribution of *Epigonus* (Epigonidae) in the world ocean. *J Ichthyol* 32:94–108  
 Abramov AA, Manilo LG (1987) *Epigonus angustifrons* sp. n., a new cardinal fish (Perciformes, Apogonidae) from submarine

- mountain ridges in the subtropical zone on the Indian Ocean. Bull Mos Soc Nat Biol Ser 92:45–48
- Ahlstrom EH, Butler JL, Sumida BY (1976) Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the North-west Atlantic. Bull Mar Sci 26:285–402
- Brauer A (1906) Die Tiefsee-Fische. I. Systematischer Teil. In: Chun C (ed) Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition “Valdivia”, 1898–99. Volume 15. Gustav Fischer, Jena, pp 1–432, pls 1–18
- Dieuzeide R (1950) Sur un *Epigonus* nouveau de la Méditerranée (*Epigonus denticulatus* nov. sp.). Bull Trav Publ Sta Aquic Peche Castiglione 2:87–105
- Gon O (1985) Two new species of the deepsea cardinalfish genus *Epigonus* (Perciformes, Apogonidae) from the Hawaiian Islands, with a key to the Hawaiian species. Pac Sci 39:221–229
- Gon O (2003) Epigonidae, deepwater cardinalfishes. In: Carpenter KE (ed) FAO species identification guide for fishery purposes. The living marine resources of the western central Atlantic. Volume 3: Bony fishes part 2 (Opistognathidae to Moridae). FAO, Rome, pp 1392–1394
- Goode GB, Bean TH (1881) Description of a new species of fish, *Apogon pandionis*, from deep water off the mouth of Chesapeake Bay. Proc U S Nat Mus 4:160–161
- Goode GB, Bean TH (1896) Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers Blake, Albatross, and Fish Hawk in the north-western Atlantic, with an atlas containing 417 figures. Spec Bull U S Natl Mus 2:1–553
- Ida H, Okamoto M, Sakaue J (2007) *Epigonus cavaticus* (Teleostei: Perciformes), a new epigonid fish from Palau, western Central Pacific. Ichthyol Res 54:131–136
- Idrees Babu KK, Akhilesh KV (2020) *Epigonus indicus*, a new species of deepwater cardinalfish (Perciformes: Epigonidae) from the Indian Ocean. J Ocean Sci Found 36:20–27
- Jordan DS, Jordan EK (1922) A list of the fishes of Hawaii, with notes and descriptions of new species. Mem Carnegie Mus 10:1–92
- Krupp F, Zajonz U, Khalaf MA (2009) A new species of the deepwater cardinalfish genus *Epigonus* (Perciformes: Epigonidae) from the Gulf of Aqaba, Red Sea. Aqua 15:223–227
- Mabee PM (1988) Supraneural and predorsal bones in fishes: development and homologies. Copeia 1988:827–838
- Mayer GF (1974) A revision of the cardinalfish genus *Epigonus* (Perciformes, Apogonidae), with descriptions of two new species. Bull Mus Comp Zool 146:147–203
- Okamoto M (2011) A new species of deepwater cardinalfish, *Epigonus mayeri*, from the eastern Central Atlantic, and redescription of *Epigonus heracleus* Parin and Abramov 1986 (Perciformes: Epigonidae). Ichthyol Res 58:101–108
- Okamoto M (2012) Two new species of the genus *Epigonus* (Perciformes: Epigonidae) from the South Pacific, with a definition of the *Epigonus constanciae* group. Ichthyol Res 59:242–254
- Okamoto M (2015) *Epigonus draco*, a new species of deepwater cardinalfish (Perciformes: Epigonidae) from the Western Pacific. Species Divers 20:121–127
- Okamoto M (2018) First records of two deepwater cardinalfishes (Perciformes: Epigonidae), *Epigonus lifouensis* and *E. pectinifer*, from Indonesia, eastern Indian Ocean. Species Divers 23:243–248
- Okamoto M, Bartsch P, Motomura H (2012) *Epigonus merleni*, a junior synonym of *Epigonus macrops* (Actinopterygii: Perciformes: Epigonidae). Species Divers 17:123–126
- Okamoto M, Chen W-J, Motomura H (2020) New distributional records of three deepwater cardinalfishes *Epigonus angustifrons*, *E. denticulatus*, and *E. exodon* (Perciformes: Epigonidae) in the South Indian Ocean. Cybium 44:165–168
- Okamoto M, Gon O (2018) A review of the deepwater cardinalfish genus *Epigonus* (Perciformes: Epigonidae) of the Western Indian Ocean, with description of two new species. Zootaxa 4382:261–291
- Okamoto M, Miyamoto K (2022) First record of the epigonid fish *Epigonus elongatus* off the coast of Okinawa Island, Japan. Jpn J Ichthyol 69:43–50
- Okamoto M, Motomura H (2011) *Epigonus carbonarius*, a new species of deepwater cardinalfish (Perciformes: Epigonidae) from the Marquesas Islands, with a redefinition of the *Epigonus oligolepis* group. Ichthyol Res 58:155–160
- Okamoto M, Motomura H (2012) *Epigonus exodon*, a new species of deepwater cardinalfish (Teleostei: Perciformes: Epigonidae) from Réunion, western Indian Ocean. Zootaxa 3453:84–88
- Okamoto M, Motomura H (2013) Two new species of deepwater cardinalfish from the Indo-Pacific, with a definition of the *Epigonus pandionis* group (Perciformes: Epigonidae). Ichthyol Res 60:301–311
- Parin NV, Abramov AA (1986) Two new species of the bathypelagic fishes of the genus *Epigonus* (Apogonidae) from the western tropical part of the Indian Ocean. Byull Mosk Obsh Ispyt Prir Otd Biol 91(3):53–57
- Rafinesque CS (1810) Indice d’ittologia siciliana; ossia, catalogo metodico dei nomi latini italiani, e siciliani dei pesci, che si rinvencono in Sicilia: disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione di alcuni nuovi pesci siciliani. Presso Giovanni del Nobolo, Messina
- Risso A (1810) Ichthyologie de Nice, ou histoire naturelle des poissons du département des Alpes Maritimes. Chez F Schoell, Paris
- Sabaj MH (2020) Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669
- Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. Can J Zool 69:82–90
- Weigt LA, Driskell AC, Baldwin CC, Ormos A (2012) DNA barcoding fishes. Chapter 6. In: Kress WJ, Erickson DL (eds) DNA barcodes: methods and protocols. Humana Press, New Jersey, pp 109–126

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.