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New species of *Monomitopus* (Ophidiidae) from Hawai‘i, with the description of a larval coiling behavior

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Abstract

In 1985, Carter and Cohen noted that there are several yet-to-be described species of *Monomitopus* (Ophidiidae), including one from Hawai‘i. Recently, blackwater divers collected a larval fish off Kona, Hawai‘i, similar to the previously described larvae of *M. kumae*, but DNA sequence data from the larva does not match any of the six previously sequenced species within the genus. Within the Smithsonian Institution's National Museum of Natural History Ichthyology Collection, we find a single unidentified adult specimen of *Monomitopus* collected North of Maui, Hawai‘i in 1972 whose fin-ray and vertebral/myomere counts overlap those of the larval specimen. We describe this new Hawaiian species of *Monomitopus* based on larval and adult characters. Additionally, blackwater photographs of several species of *Monomitopus* show the larvae coiled into a tight ball, a novel behavior to be observed in cusk-eels. We describe this behavior, highlighting the importance of blackwater photography in advancing our understanding of marine larval fish biology.

Key words: Blackwater, COI, Ianniello's coil, Integrative taxonomy, *Monomitopus agassizii*

要旨 (Japanese)

Carter & Cohen (1985) は、クマイタチウオ属(アシロ科)にはまだ記載されていない種がいくつかあり、その中にはハワイ近海の種も含まれていると指摘した。近年、ブラックウォーターダイバーがハワイ島コナ沖で、これまでに報告されているクマイタチウオ *Monomitopus kumae*の仔魚に似た種を採集したが、この個体のDNA配列データは、同属の中でこれまでに配列が決定された6種のどれとも一致しなかった。また、スミソニアン協会の米国立自然史博物館の魚類コレクションから、1972年にハワイ州マウイ島北部で採集され、先述の仔魚標本と鰭条数および脊椎•筋節数が一致するクマイタチウオ属の未同定の成魚標本1個体を発見した。この仔魚標本と成魚標本の両方の特徴に基づき、クマイタチウオ属の新種として記載した。また、クマイタチウオ属数種のブラックウォーターの写真では、仔魚が球状に丸くなった状態で写っており、これはアシロ科魚類では観察されていなかった新しい行動であった。この行動パターンについて記載し、海洋仔稚魚の生態の理解を深める上でのブラックウォーター写真の重要性を改めて強調する。

Introduction

Monomitopus is a circumglobal genus of cusk-eels (Ophidiidae) found between 150 and 1600 m in tropical and subtropical seas (Nielsen *et al.* 1999). Alcock (1890) described the genus to separate *Monomitopus nigripinnis* from species in the genus *Sirembo* based on fewer pseudobranch filaments compared to congeners. Along with a rudimentary pseudobranch, species of *Monomitopus* can be differentiated from other cusk-eels by an eye diameter

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equal to or slightly shorter than snout, a strong opercular spine, two or three spines at the lower angle of the preopercle (Nielsen *et al.* 1999), and one basibranchial 3 tooth plate that extends anteriorly above basibranchials 1 and 2. The genus currently includes 14 species divided into three groups based on shape of the head, ossification of the opercular bones, and strength of preopercular spines (see Carter & Cohen 1985): the *M. nigripinnis* group (*M. agassizii*, *M. conjugator*, *M. garmani*, *M. malispinosus*, *M. metriostoma*, *M. nigripinnis*, and *M. vitiazi*), diagnosed by a downward-sloped head, poorly ossified opercular bones, and weak, flap-like spines on the preopercle; the *M. pallidus* group (*M. americanus*, *M. magnus*, and *M. pallidus*), diagnosed by a relatively straight dorsal profile, well ossified opercular bones, and distinct strong spines on the preopercle; and the *M. torvus* group (*M. kumae*, *M. longiceps*, *M. microlepis*, and *M. torvus*), diagnosed by a relatively straight dorsal profile, intermediately ossified opercular bones, and moderately distinct spines on the preopercle relative to the other two groups. In their description of *M. magnus*, Carter & Cohen (1985: 86) noted that several other species of *Monomitopus* have yet to be described, including an "unidentified specimen from Hawaii (BPBM)" that belongs to the *M. nigripinnis* group. Neither catalog number nor additional information about this Hawaiian specimen is listed, and there has yet to be a confirmed specimen of *Monomitopus* collected from Hawaiʻi or cataloged in the Bernice P. Bishop Museum Ichthyology Collection (BPBM).

Okiyama (2014) described the larval form of *M. kumae* from one preflexion (5.9 mm standard length [SL]) and one postflexion (16.0 mm SL) specimen. These larvae have several characters that distinguish them from other ophidiid larvae, including large head that is equal to or exceeds depth of body, small eyes, large oblique mouth, short tapering body, broad pectoral-fin bases, and a rudimentary pelvic-fin ray. Okiyama (2014, translated by A. Nonaka) noted little pigmentation on the larvae, with melanophores above the brain case, beneath the dentary, and near the gut. Although not listed in the description, the illustration of the 16.0 mm SL specimen (Okiyama 2014: 432) also shows a distinct banding pattern at the bases of the dorsal- and anal-fin rays, but it is unclear if this pattern continues distally along the fin rays or is limited to the bases. Since this original description of larval *M. kumae*, no other larvae of *Monomitopus* have been described.

Blackwater diving, photography, community science, and DNA barcoding efforts have allowed for new larval behaviors to be observed (Pastana *et al.* 2022) and larval forms to be identified (e.g., Nonaka *et al.* 2021; Girard *et al.* 2023). In 2021, blackwater divers photographed and collected a 14.4 mm SL larva with a large head and tapering body off the coast of Kona, Hawaiʻi (Figs. 1 and 2A). Several phenotypic characters found in the larva are similar to those described by Okiyama (2014) for *M. kumae*, and genotypic characters identify this specimen as a species of *Monomitopus* (Fig. 2B). However, the DNA barcode from the larva does not match any of the six previously sequenced species within the genus, and no species of *Monomitopus* are known to occur in Hawaiʻi. During our examination of adult specimens, we found a single unidentified specimen of *Monomitopus* collected North of Maui, Hawaiʻi, in 1972 within the Smithsonian Institution's National Museum of Natural History Vertebrate Zoology Fishes Collection (USNM) that overlaps in fin-ray and vertebral/myomere counts of the larval Hawaiian specimen (Figs. 1 and 2A, see below). This adult specimen was sent to the USNM from Hawaiʻi between the late 1970's and early 1980's, cataloged into the USNM collection in September 1984 (USNM 267749), and is the unidentified specimen and new species mentioned by Carter & Cohen (1985; their paper was accepted in April 1984) but listed as a part of the BPBM collection in their publication. We describe this new species of *Monomitopus*, the first from Hawaiian waters, based on these larval and adult specimens. Additionally, blackwater photographs of the Hawaiian larva, two newly identified larvae of *M. agassizii* (Fig. 3), and several uncollected larval *Monomitopus* show the larvae contorting their bodies into a tight coil; a novel behavior to be observed in cusk-eels. We describe this behavior, adding to the growing body of literature that highlights the importance of blackwater photography in advancing our understanding of marine-larval-fish biology.

Materials and methods

Imaging and capture of larval specimens. Larvae were photographed during blackwater scuba dives (see Nonaka *et al.*, 2021) using a Nikon D500 camera with a 60 mm macro lens within a waterproof housing, two 2000-lumen focus lights, and two Ikelite external strobes. A subset of photographed larvae were captured at depth using a vessel of sea water and transferred to a solution of laboratory-grade 95% ethanol at the surface (see Nonaka *et al.*, 2021). See Declarations section for ethics and permitting information.

Morphological identification, examination, and laboratory imaging of larvae and adults. Three larval and over 90 adult specimens were examined representing all described species of *Monomitopus*. All specimens examined, along with their lengths and museum catalog numbers, are listed in Appendix 1. Museum codes follow Sabaj (2020) except for NMNH referring to non-Fishes Division personnel and resources at the National Museum of Natural History, Smithsonian Institution and DPND referring to specimens collected through the DEEPEND project (Nova Southeastern University). Specimens were photographed using equipment listed in Girard *et al.* (2020). Specimens were x-rayed to view osteology using the x-ray equipment listed in Girard *et al.* (2023).

TABLE 1. Genetic vouchers and sequences. Taxa followed by an "*" used in phylogenetic analysis.

Species	Museum Voucher	BOLD Process ID	GenBank Accession Number
Monomitopus ainonaka **sp. nov.***	USNM 454563	MNSP001-23	OR263969
*Monomitopus agassizii**	DPND 4535	DPND2200-16	MG856452
Monomitopus agassizii	DPND 5497	DPND3187-17	MT323592
Monomitopus agassizii	USNM 407074	MOCA074-12	
Monomitopus agassizii	USNM 407132	MOCA132-12	
Monomitopus agassizii	USNM 407201	MOCA201-12	
Monomitopus agassizii	USNM 407440	MOCA440-12	
Monomitopus agassizii	USNM 407460	MOCA460-12	
Monomitopus agassizii	USNM 407651	MOCA651-12	
*Monomitopus agassizii**	USNM 465352	MNSP002-23	OR263968
*Monomitopus agassizii**	USNM 465385	MNSP003-23	OR263967
Monomitopus kumae	ASIZ P.0801262	FTWS671-09	KU943155
*Monomitopus kumae**	ASIZ P.0806597	ZOSKT341-16	KU943169
Monomitopus malispinosus	USNM 421240	MOP247-12	MF956825
Monomitopus malispinosus	USNM 421249	MOP248-12	MF956826
Monomitopus malispinosus	USNM 421300	MOP578-12	MF956820
Monomitopus malispinosus	USNM 421441	MOP475-12	MF956829
Monomitopus malispinosus	USNM 421464	MOP576-12	MF956822
Monomitopus malispinosus	USNM 421530	MOP487-12	MF956823
Monomitopus malispinosus	USNM 422492	MOP717-12	MF956827
*Monomitopus malispinosus**	USNM 422509	MOP715-12	MF956819
Monomitopus malispinosus	USNM 422552	MOP715-12	MF956821
Monomitopus malispinosus	USNM 422624	MOP577-12	MF956828
Monomitopus malispinosus	USNM 435794	MOP609-12	MF956824
*Monomitopus pallidus**	ASIZ P.0801575	FTW909-09	KU885677
*Monomitopus torvus**	USNM 422497	MOP773-12	MF956818
*Monomitopus vitiazi**	NMV A29720-10	FOAO2244-20	
*Selachophidium guentheri**	SAIAB uncat.	TZMSC402-05	JF494490
*Sirembo imberbis**		GBGCA4393-13	JQ681480

Taxon sampling and identification using molecular characters. Protocols for tissue sampling, DNA extraction, PCR, and sequencing cytochrome c oxidase subunit 1 (COI) follow the methods described in Nonaka *et al.* (2021) and Weigt *et al.* (2012) using primers from Baldwin *et al.* (2009). Sequence contigs were built, edited, and assembled using Geneious, vers. 11.1.5 (Kearse *et al.* 2012) and deposited on both GenBank ([OR263967–OR263969]) and BOLD (MNSP001-23–MNSP003-23). Each newly generated COI sequence was compared to sequences in the BOLD SYSTEMS Identification Engine "All Barcode Records on BOLD" dataset (Ratnasingham & Hebert, 2007; comparisons as of 8 March 2023). Genetically similar sequences and specimen vouchers were then examined, when available (see Appendix 1, Table 1), to confirm voucher identification. A subset of these sequences were downloaded for phylogenetic analysis (see Table 1) and collated into a single file with newly sequenced larvae (Fig. 2B). This file was aligned with MAFFT vers. 7 (Katoh & Standley 2013) within Geneious, and the resulting alignment contained 11 terminals, was 652 base pairs (bps) in length (~96% complete at the level of individual bps) and contained 116 parsimony-informative sites. The matrix was partitioned and analyzed using IQ-Tree vers. 2.2.0 (i.e., MFP + MERGE, Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017; Minh *et al.* 2020) following the methods in Girard *et al.* (2023). Analyses were rooted on *Selachophidium guentheri*.

Monomitopus ainonaka **sp. nov.**

English name: Ai's cusk

urn:lsid:zoobank.org:act:F9B58F1C-89E3-4A1C-8D4C-D00BFC93CBE6

Holotype. USNM 267749; 135 mm SL (Figs. 1A–B, 2; Table 2).

Collection information: 16 July 1972; 768–796 m depth. Station data from NOAAS *Townsend Cromwell* lists collection as North of Maui, Hawai'i, 21º 09' N 156º 11' W (Fig. 2A). Hand-written label found with the specimen lists collection at 21° 07' N 156° 12' W, but we think this is inaccurate based on the station information from preceding and subsequent trawls of cruse 59.

Counts: 105 dorsal-fin rays, 92 anal-fin rays, 35 pectoral-fin rays, 8 caudal-fin rays, 1 pelvic-fin ray, 12 precaudal vertebrae, 62 total vertebrae, 8 branchiostegals (6 epihyal, 2 ceratohyal), 5 rudimentary gill rakers on hypobranchial 1, 17 elongate gill rakers on ceratobranchial 1 (including angle), 4 club-like gill rakers on epibranchial 1, anteriormost anal-fin ray ventral to 18th dorsal-fin ray and 14th vertebra, anteriormost dorsal-fin ray above fourth vertebra.

Measurements as % SL: 22.5 head length, 4.3 snout length, 11.4 upper jaw, 5.2 horizontal eye diameter, 36.0 preanal distance, 22.3 predorsal distance, 17.0 distance from base of pelvic-fin ray to vent, 16.2 body depth at level of vent, 12.1 pelvic-fin ray length, 6.2 interorbital width, 12.9 postorbital length.

Diagnosis. A species of *Monomitopus* with weak, flap-like spines on preopercle, downward-sloped dorsal profile between eye and origin of the dorsal fin as adult. It can be further differentiated from species of *Monomitopus* in the *M. nigripinnis* group occurring in the Pacific (i.e., *M. garmani* [Celebes to New Caledonia] and *M. malispinosus* [Eastern Central Pacific]) by greater numbers of dorsal-fin rays (105 vs. 94–103 in *M. garmani*; 96–99 in *M. malispinosus*), anal-fin rays (92 vs. 76–87 in *M. garmani*; 81–84 in *M. malispinosus*), pectoral-fin rays (35 vs. 28–32 in *M. garmani*; 26–29 in *M. malispinosus*) and smaller ratio of eye diameter relative to head length (4.4 vs. 4.6–5.6 in *M. garmani*; 4.6–4.9 in *M. malispinosus*; see Table 2).

Adult description. Head compressed, dorsal margin sloped downward to snout. Nostrils widely separated, anterior with tube-like flap, posterior close to eye. Eye longer than deep, about four times into head length, film of tissue covering eye. Infraorbital sensory canal not evident. Broad flap of tissue covering dorsal half of maxilla. Mouth large, slightly oblique; lower jaw inferior. Distal end of maxilla dorsoventrally expanded with concave posterior margin. Supramaxilla present. Premaxilla and dentary with small, numerous, villiform teeth all subequal in size. Intraoral teeth similar in size to oral teeth. Palatine tooth patch elongate, rounded anteriorly, tapering posteriorly; vomerine tooth patch with anterior bulbous patch, tapering to lateral arms. Dentition interrupted across upper and lower jaw symphyses. Eight branchiostegals (full complement), 2 on ceratohyal. One elongate basibranchial 3 tooth plate posterior to basihyal, anteriorly broad and tapering posteriorly, overlapping basibranchials 1 and 2. Tooth plates on epibranchials 2, 3, and 4. Pseudobranch short and rudimentary, with two filaments. Preopercle with four weak, flap-like spines; easily bent if probed. Opercle strongly bent at acute angle with posterior spine piercing skin. Opercular spine narrowly ovoid in cross-section. Opercular tissue connected dorsally to body via broad flap of skin. Head scaleless, body with deciduous scales. Many lateral-line scales missing, but canal appears to end near level of anus, as in other species of *Monomitopus* (see Carter & Cohen 1985). Pectoral fin shallow, all fin rays subequal. Pelvic girdle minute, inserts immediately behind cleithral symphysis. Single pelvic-fin ray thin with broad base. Gut moderate in size. Dorsal- and anal-fin rays approximately subequal in length to each other and along each fin. Caudal-fin rays elongate with truncate posterior margin. Body pale brown, speckled with melanophores; opercular tissue dark.

TABLE 2. Counts and measurements for species of *Monomitopus*. Values in parentheses indicate counts or measurements from holotype. Values in brackets indicate counts or measurements from syntype. In-table citations for holotype counts: [1]Nielsen, 1971; [2]Garman, 1899; [3]Alcock, 1889.

Species of *Monomitopus*	Dorsal-fin rays	Anal-fin rays	Pectoral-fin rays	Caudal-fin rays	Precaudal vertebrae	Total vertebrae	Elongate gill rakers on lower arm of first gill arch (including angle)	Horizontal eye diameter in head length
M. ainonaka **sp. nov.**	(105)	(92)	35 (35)	(8)	12 (12)	(62)	(17)	(4.4)
M. agassizii	99–107	83–89	31–34	7–8	12–14	61–64	17–19	4.0–4.2
M. americanum [1]	100–108 (102)	82–89 (83)	28–32 (29–30)	8 (8)	13–14 (14)	59–63 (62)	16–17 (16)	3.8
M. conjugator	(90) [96]	(72) [76]	(28) [34]	[8]	[13]	[59]	(12) [14]	4.3–4.7 [4.3]
M. garmani	92–103 (96)	76–87 (80)	28–32 (31)	7–8 (8)	13–14 (13)	57–62 (59)	(22)	4.6–5.6 (5.3)
M. kumae	100–105 (105)	85–88 (88)	29–33 (31)	(8)	12–14 (14)	55–64 (62)	(18–19)	4.6–6.3 (6.3)
M. longiceps	(97)	(82)	(28)	(9)	(12)	(57)	(22)	(4.9)
M. magnus	104–109 (109)	85–92 (92)	27–31 (29)	8 (8)	15 (15)	61–65 (65)	10–11 (10)	4.6–5.3 (5.0)
M. malispinosus [2]	96–99 (99)	82 (82)	26–29 (26)	8 (8)	12	58	18 (18)	4.6–4.9 (4.8)
M. metriostoma	95–103	79–87	27–32	8	12–13	58–63	17–18	3.6–4.2
M. microlepis	97–102 (98)	81–84 (82)	29–31 (28)	8 (8)	14 (14)	58–61 (60)	(17)	4.2–5.6 (5.6)
M. nigripinnis [3]	91–95 (95)	76–85 (85)	27–30 (28)	8	12–13	54	17–18	3.9–4.8
M. pallidus	87–96 (93)	71–77 (76)	26–28 (28)	7–8 (7)	13 (13)	53–57 (55)	(16)	3.4–4.0 (3.7)
M. torvus [2]	98–111 (109)	83–95	28–33 [33]	8	12–15 [13]	58	17–18 (18) [17]	4.0–4.6
M. vitiazi [1]	93–98 (93)	78–84 (78)	28–33 (28–29)	8 (8)	13 (13)	56–58 (56)	13–14 (13)	4.4–4.9 (4.9)

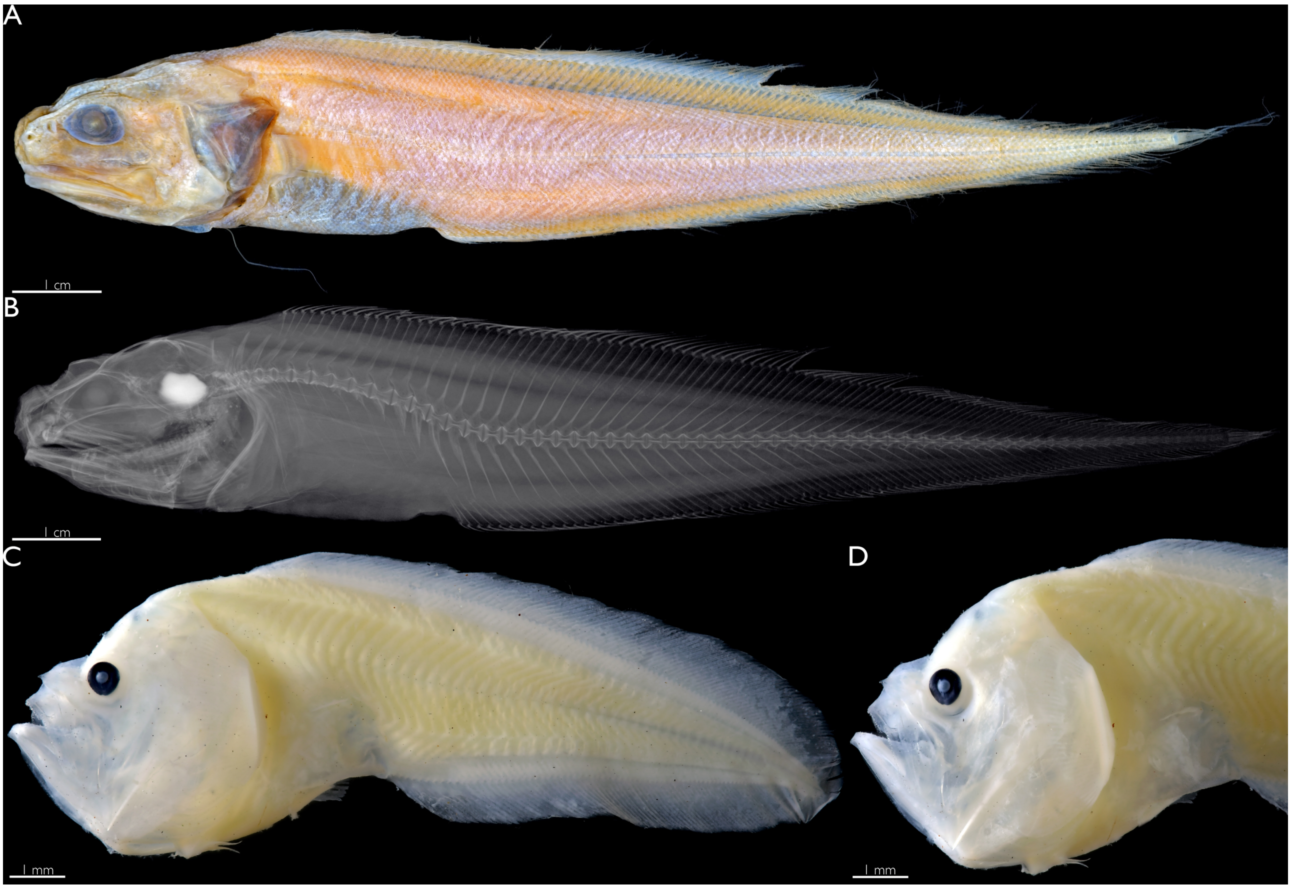

FIGURE 1. Adult and larva of *Monomitopus ainonaka* **sp. nov.** from the Hawaiian Islands. A) USNM 267749 holotype. B) Radiograph of holotype. C) Larva, USNM 454563, captured by A. and N. Deloach offshore of Kona, Hawai'i, 11 November 2021. D) Close-up of USNM 454563 head.

Non-type larval specimen. USNM 454563; 14.4 mm SL; preflexion; 11 November 2021; off Kona, Hawai'i; 0–18 m over a depth 1500 m (Figs. 1C–D, 2A, 4A).

Counts: 100+ dorsal-fin rays (posteriormost rays undifferentiated), 82+ anal-fin rays (posteriormost rays undifferentiated), 35 pectoral-fin rays, caudal-fin rays undifferentiated, 1 pelvic-fin ray, 12 precaudal myomeres, 55+ total myomeres (posteriormost myomeres indiscernible), anteriormost anal-fin ray ventral to 17th dorsal-fin ray, anteriormost dorsal-fin ray above fourth myomere.

Larval description. Head large, deeper than long, body tapering posteriorly to narrow caudal fin. Eye small, deeper than wide, ovoid. Maxilla and premaxilla at oblique upturned angle. Premaxilla and dentary with small, distantly spaced teeth. Distal end of maxilla dorsoventrally expanded, posterior margin convex. Posterior tip of premaxilla nearly reaching posterior margin of maxilla. Supramaxilla present. Large rostral cartilage attached to ascending process of premaxilla. Nostrils in close proximity, anterior to eye. Symphysis of dentary with slight ventral expansion. Opercular series without spines. Body and head scaleless. Dorsal fin inserting in line with pectoral-fin base. Pectoral fin large, fan like, with broad base. Pectoral-fin membrane between each ray entire. Pelvic-fin ray minute, inserting immediately behind cleithral symphysis. Gut moderate, internal to body and lacks exterilium morphology of some other larval ophidiids (Fraser & Smith, 1974; Fahay & Nielsen, 2003; Okiyama, 2014). Internal gut loops not evident. Anus just anterior to anal fin with no external extension. Dorsal, anal, and caudal fins confluent. Dorsal- and anal-fin rays approximately subequal in length to each other and along each fin. Larval caudal fin not fully formed. Melanophores few and minute on head and body, distributed randomly across larva.

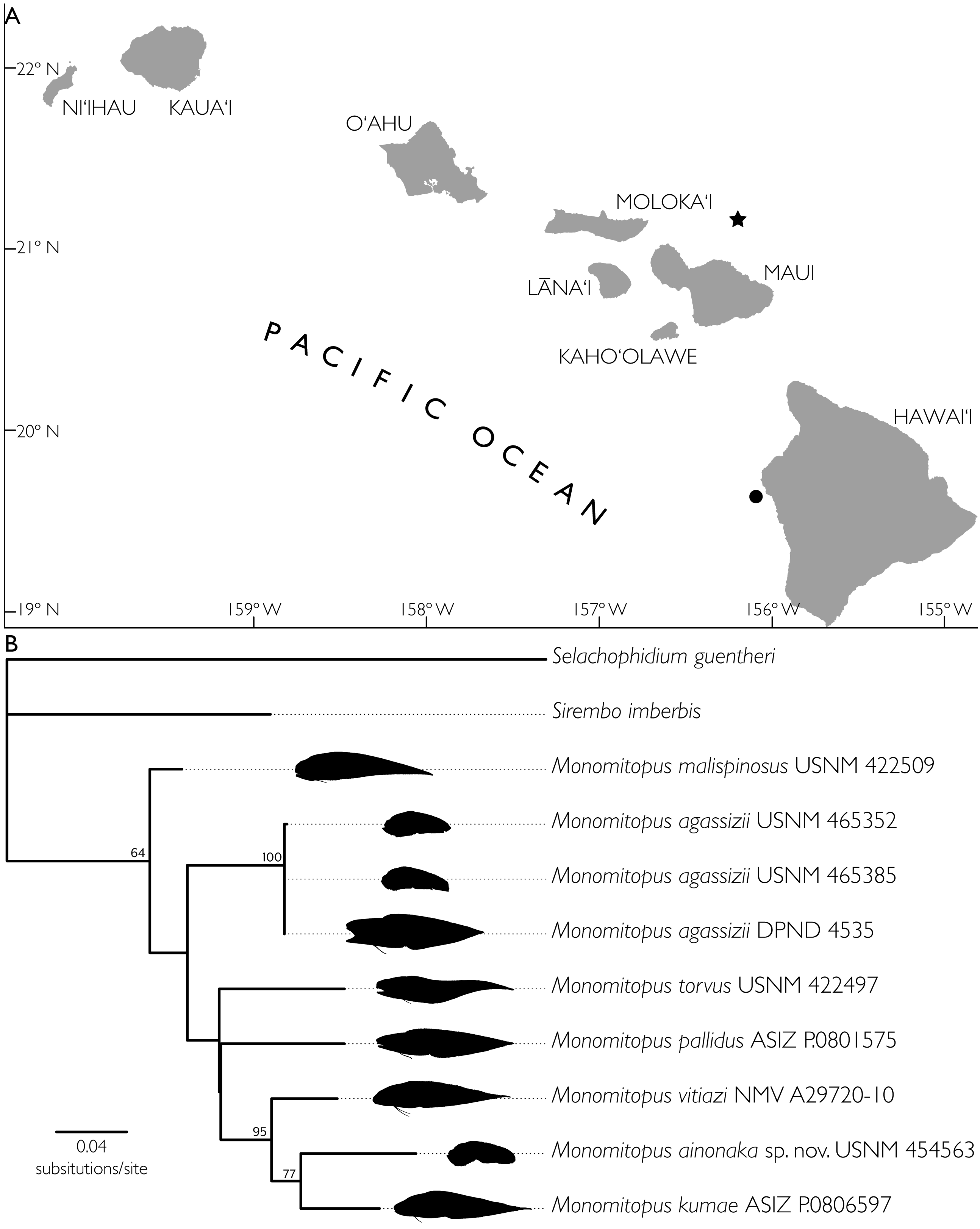

FIGURE 2. A) Map of collection localities for *M. ainonaka* **sp. nov.** Star indicates locality of holotype (USNM 267749). Circle indicates locality of larva (USNM 454563). B) Phylogeny of *Monomitopus* spp. Bootstrap values >50% listed. Silhouettes indicate developmental stage of the genetic voucher.

FIGURE 3. Adult and larvae of *Monomitopus agassizii* from the Western Atlantic. A) USNM 407201, a genetically matching adult to newly identified larvae USNM 465352 and USNM 465385. B) USNM 465352. C) Close-up of USNM 465352 head. D) USNM 465385. E) close-up of USNM 465385 head.

Following description based on *in-situ* image of larval specimen. Specimen speckled with melanophores across head and body, distributed evenly across the body, denser above braincase. Dorsal and anal fins banded, with dorsal-fin-ray pattern: three-to-four rays pigmented, three-to-four rays lacking pigment, etc.; anal-fin-ray pattern, four-to-five rays pigmented, three-to-four rays lacking pigment, etc.

Genotypic data. The barcode sequence from the larva ([OR263969]) was compared to sequences from six of the 14 species of *Monomitopus* and was ≥6.5% divergent (see Table 1 for BOLD and GenBank accession numbers). Our phylogenetic analysis resulted in a single optimal topology (ln L = -2418.422) with *M. ainonaka* in a clade of Pacific species of *Monomitopus*, sister to *M. kumae*. Despite the moderate branch support, all tree searches resulted in the same topology shown in Fig. 2B but with different branch lengths.

Distribution. Both larval and adult specimens have been collected from waters surrounding the Hawaiian Islands, and this is the only confirmed locality for this species. Unidentified individuals of *Monomitopus* have been recorded from Wake Island as well as Howland and Baker Islands at depths of 1000–3000 meters by NOAA Ocean Exploration (2016, 2017), but these individuals were not collected. We have examined both still and video images of these individuals, and they appear more similar to *Monomitopus garmani* or *M. microlepis* based on fin-ray counts (i.e., ~102–103 dorsal-fin rays, ~89–90 anal-fin rays, ~30 pectoral-fin rays) and horizontal eye diameter in head length (~5.1–5.5; see Table 2) than to the new species described from Hawai'i. Additional sampling from these regions is needed to understand the full distributions of species in this genus.

Etymology. Named for Ai Nonaka (USNM) for her interest in ophidiid larvae and dedication to the discovery, identification, and curation of larval fishes.

Larvae of *Monomitopus agassizii*

USNM 465352, 15.3 mm SL; flexion; collected 7 May 2021; off West Palm Beach, Florida; 13–20 m depth (Figs. 3B–C, 4B–C). USNM 465385, 18.2 mm SL; postflexion; 24 March 2021; off West Palm Beach, Florida; 0–18 m depth (Figs . 3D–E, 4F–H).

Counts: dorsal-fin rays 99–104; anal-fin rays 84–85; pectoral-fin rays 31–34; pelvic-fin rays 1; caudal-fin rays 8; precaudal myomeres ~14; posterior myomeres indiscernible.

Description. General morphology same as larval *M. ainonaka* (see above). Differences include: posterior margin of maxilla with large number of melanophores; *in situ* photos of specimens show no medial-fin-ray banding.

Genotypic data. The COI barcode sequences from the larvae ([OR263968–OR263969]) were compared to barcodes of six of the 14 species of *Monomitopus* (see Table 1) and were 99.7–100% the same to adult specimens of *M. agassizii*. Our phylogenetic analysis of COI (see above) recovers all samples of *M. agassizii* in a clade sister to *M. ainonaka, M. kumae*, *M. pallidus*, *M. torvus*, and *M. vitiazi* (Fig. 2B).

Coiling behavior in larval *Monomitopus*

Like many cusk-eel larvae, larval *Monomitopus* are very rare, with as few as five seen in >1000 blackwater dives over a ten-year interval in eastern Florida, one seen in 150 blackwater dives over a three-year interval in Anilao, Philippines, and one seen (and fortuitously collected) in >90 dives in Kona, Hawai‘i (2021; A. Deloach, D. Devers, L. Ianniello, and S. Kovacs, pers. comm). All larval *Monomitopus*, including *M. agassizii* (Florida; Fig. 4B–C, 4F–P), *M. ainonaka* (Hawai‘i; Fig. 4A), *M.* cf. *magnus* (Florida; Fig 4E), and *M.* sp. (Philippines, Fig. 4D) were noticed by blackwater divers because of their distinctly coiled bodies. We name this coiling behavior ‘Ianniello’s coil’ after L. Ianniello for documenting a long behavioral sequence of *M. agassizii* and for her willingness to share her knowledge and images of larval fishes from the blackwater. Larval *Monomitopus* form Ianniello’s coil by bending the body posterior to the gut towards the head. When the body is bent approximately in half, the tail is then directed dorsally at the level of the opercle, with the caudal tip wrapping over the body between the head and anteriormost dorsal-fin rays, forming a complete and overlapping coil. All larvae observed forming Ianniello’s coil kept their heads steady, moving their tails over their heads. Divers spent 1–5 minutes observing and photographing individual larvae, all of which drifted with the current in Ianniello’s coil and did not appear to perform this behavior in response to the diver presence. No larvae appeared alarmed or attempted to flee during observation or capture. While most of the larvae remained in right-handed (i.e., dextral) coils during all observations and capture (Fig. 4), two *M. agassizii* observed for 3–5 minutes (USNM 465385, Fig. 4F–H; uncaptured larva, Fig. 4I–P) transitioned between dextral and left-handed (i.e., sinistral) coils. For USNM 465385, the larva was first observed in a dextral coil (Fig. 4F) before briefly uncoiling (Fig. 4G) and forming a sinistral coil (Fig. 4H) over a 200 second interval (D. Devers, pers. comm.). The uncaptured larva was observed on 2 March 2021 off West Palm Beach, Florida at 9–12 m depth (Fig. 4I–P). This larva repeatedly switched coil handedness over a three-minute interval (all times local): 21:34:04 (+0 s; Fig. 4I) diver finds larva in sinistral Ianniello’s coil, 21:34:16 (+12 s; Fig. 4J) larva transitions to dextral coil, 21:34:36 (+32 s; Fig. 4K) larva uncoils, 21:34:55 (+51 s; Fig. 4L) larva transitions to sinistral coil, 21:35:01 (+57 s; Fig. 4M) larva transitions to dextral coil, 21:36:07 (+149 s; Fig. 4N–O) larva transitions to sinistral coil, 21:37:04 (+180 s; Fig. 4P) larva transitions to dextral coil (diver drifts away from larva; L. Ianniello, pers. comm.). Given these observations and that preflexion (USNM 454563), flexion (USNM 465352) and postflexion (USNM 465385) larval *Monomitopus* were all found in and remained in or repeatedly returned to Ianniello’s coil, we think these larvae are often coiled prior to settlement.

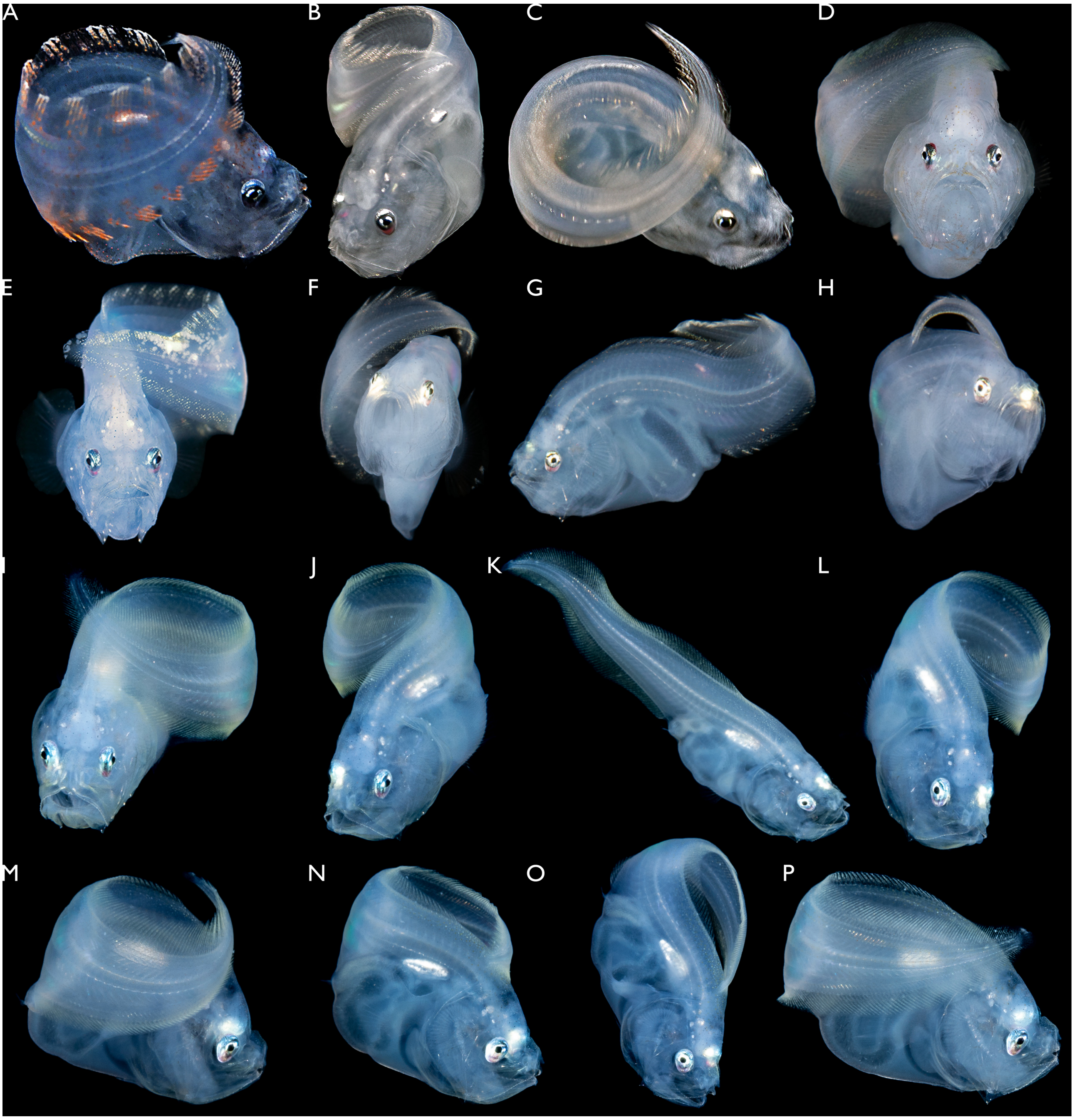

FIGURE 4. Blackwater photos of larval *Monomitopus* spp. in Ianniello's coil. A) *M. ainonaka* **sp. nov.** USNM 454563, captured and photographed by A. Deloach, N. Deloach, and S. Kovacs off Kona, Hawai'i, 11 Nov 2021. B) and C) *M. agassizii,* USNM 465352, captured and photographed by R. Collins, A. Deloach, and N. Deloach off West Palm Beach, Florida, 7 May 2021. D) *M.* sp. off Anilao, Philippines, ~10 m depth over 150 m, 5 Dec 2019. Photo © S. Kovacs. E) *M.* cf. *magnus* off West Palm Beach, Florida, ~15 m depth over 220 m, 25 Feb 2021. Photo © S. Kovacs. F–H) *M. agassizii,* USNM 465385, transitioning from dextral coil, to uncoiling, to sinistral coil, captured and photographed by D. Devers off West Palm Beach, Florida, 24 Mar 2021. I–P) Uncaptured *M. agassizii*, repeatedly transitioning coil handedness over three-minute interval (see text for time intervals), photographed by L. Ianniello off West Palm Beach, Florida, 9–12 m depth over 220 m, 2 Mar 2021. Photos © L. Ianniello.

While some larval fishes contort their bodies into "C" shapes (e.g., see various blackwater photographs of Callionymidae, Labridae, Synodontidae) completely overlapping or nearly overlapping coils have only been documented in the leptocephali of anguilliform families Chlopsidae, Congridae, Muraenidae, Nettastomatidae, and Ophichthidae (Miller 2009; Miller *et al.* 2013). Under observation, larval eels wrapped their bodies into tight spheres, several coiling one or more times around their heads (see Miller *et al.* 2013 figs. 2 and 3). This behavior was only performed in response to a perceived threat (e.g., camera lights), and Miller *et al.* (2013) proposed coiling is a form of Batesian Mimicry, whereby the leptocephali are mimicking nutritionally poor gelatinous zooplankton (e.g., cnidarians, ctenophores, salps) to avoid predation. Ianniello's coil in larval *Monomitopus* represents the first non-anguilliform larva known to form a complete coil and there are several differences between this behavior and coiling in leptocephali: larval *Monomitopus* are only able to coil their body one time (leptocephali often loop the body multiple times with caudal tip extended); larval *Monomitopus* were typically found coiled rather than coiled in response to a perceived threat; larval *Monomitopus* repeatedly returned to the coil to switch handedness. Ianniello's coil may also be an example of Batesian mimicry, similar to those described in leptocephali. Additional behavioral observations and investigations are needed to confirm this mimicry hypothesis.

Conclusion

The imaging and capture of larval fishes by blackwater divers allowed for the description of a new species of cusk-eel from Hawai'i as well as the larva of *Monomitopus agassizii*. These blackwater images also allowed for the discovery of a larval coiling behavior, novel for non-anguilliform larvae, that may be an example of Batesian mimicry. We hope that this study will continue to encourage those diving in the blackwater to document larval fishes in their natural environment and collect specimens for further study. Our examination of still images and video of *Monomitopus* recorded by NOAA Ocean Exploration indicate that at least one additional species in this genus has yet to be described from Wake, Howland, and Baker Islands. As these specimens were not collected, sampling and vouchering specimens from these regions are needed to identify additional species of cusk-eel.

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Declarations

Conflicts of interest. The authors declare no conflicts of interest.

Ethics approval. Species of fishes in this study are not listed as threatened or endangered by the IUCN Red List or CITES. All methods of capture and preservation conform to the Guidelines for the Use of Fishes in Research established by the American Fisheries Society, American Institute of Fishery Research Biologists, and American Society of Ichthyologists and Herpetologists. Larvae collected off West Palm Beach, Florida, were acquired under Florida permit SAL-21-2155A-SR. Permit not required for larval collections off Kona, Hawai'i.

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APPENDIX 1. Specimens Examined. Specimen counts followed by an "-L" indicate larval specimen. All non-larval specimens were x-rayed to view internal osteology.

Species	Museum Voucher	Count	SL	Collection Date	Collection Locality
Monomitopus ainonaka **sp. nov.**	USNM 267749 Holotype	1	135 mm	16 Jul 1972	North of Maui, Hawai'i
Monomitopus ainonaka **sp. nov.**	USNM 454563	1-L	14.4 mm	11 Nov 2021	Kona, Hawai'i
Monomitopus agassizii	USNM 44669 Paralectotype	1	130 mm	7 Feb 1885	Gulf of Mexico
Monomitopus agassizii	USNM 407074	1	181 mm	7 Jan 2011	Panama (Atlantic)
Monomitopus agassizii	USNM 407132	1	164 mm	8 Jan 2011	Panama (Atlantic)
Monomitopus agassizii	USNM 407201	1	221 mm	9 Jan 2011	Panama (Atlantic)
Monomitopus agassizii	USNM 407440	1	119 mm	16 Jan 2011	Nicaragua
Monomitopus agassizii	USNM 407460	1	153 mm	18 Jan 2011	Nicaragua
Monomitopus agassizii	USNM 407651	1	110 mm	31 Jan 2011	Belize
Monomitopus agassizii	USNM 465352	1-L	15.3 mm	7 May 2021	West Palm Beach, Florida
Monomitopus agassizii	USNM 465385	1-L	18.2 mm	24 Mar 2021	West Palm Beach, Florida
Monomitopus americanus	USNM 205095 Paratype	1	235 mm	27 Feb 1968	Brazil
Monomitopus conjugator	USNM 231713 Syntype	1	158 mm	20 Jan 1895	Laccadive Islands, India
Monomitopus garmani	USNM 74135 Holotype	1	265 mm	19 Nov 1909	Batu Daka, Indonesia
Monomitopus garmani	USNM 99102 Paratype	2	147–153 mm	27 Nov 1909	North Maluku, Indonesia
Monomitopus garmani	USNM 99103 Paratype	2	143–155 mm	16 Dec 1909	North Island, Indonesia
Monomitopus garmani	USNM 99104 Paratype	2	136–177 mm	16 Dec 1909	North Island, Indonesia
Monomitopus garmani	USNM 99108 Paratype	1	201 mm	16 Dec 1909	North Island, Indonesia

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APPENDIX 1. (Continued)

Species	Museum Voucher	Count	SL	Collection Date	Collection Locality
Monomitopus garmani	USNM 99112 Paratype	1	259 mm	20 Nov 1909	Sulawesi, Indonesia
Monomitopus garmani	USNM 99260 Paratype	6	85–109 mm	27 Nov 1909	North Maluku, Indonesia
Monomitopus kumae	FMNH 58844 Holotype	1	363 mm	1922	Misaki, Japan
Monomitopus kumae	USNM 149250	1	198 mm	29 Aug 1906	Honshu, Japan
Monomitopus kumae	USNM 150437	1	287 mm	30 Aug 1906	Honshu, Japan
Monomitopus longiceps	USNM 74134 Holotype	1	305 mm	8 Aug 1908	Luzon, Philippines
Monomitopus magnus	USNM 228226 Paratype	4	362–548 mm	9 Nov 1961	North of Cal Sal Bank, Florida
Monomitopus magnus	USNM 262507 Holotype	1	425 mm	9 Nov 1961	North of Cal Sal Bank, Florida
Monomitopus malispinosus	MCZ 28649 Holotype	1	-	10 Mar 1891	Panama (Pacific)
Monomitopus malispinosus	USNM 208279	1	150 mm	1 Feb 1972	Peru
Monomitopus malispinosus	USNM 267588	1	179 mm	2 Mar 1888	Ecuador
Monomitopus malispinosus	USNM 421240	1	173 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 421249	1	171 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 421300	1	183 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 421441	1	169 mm	4 Dec 2010	Costa Rica
Monomitopus malispinosus	USNM 421464	1	219 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 421530	1	197 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 422492	1	175 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 422509	1	144 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 422552	1	141 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 422624	1	205 mm	12 Nov 2010	Panama (Pacific)
Monomitopus malispinosus	USNM 435794	1	286 mm	21 Nov 2010	Panama (Pacific)
Monomitopus metriostoma	USNM 226611	1	103 mm	31 May 1964	Cote d'Ivoire
Monomitopus metriostoma	USNM 226613	3	107–176 mm	30 May 1964	Cote d'Ivoire
Monomitopus metriostoma	USNM 226614	19	78–167 mm	4 Jul 1964	Gulf of Guinea, off Liberia
Monomitopus metriostoma	USNM 267756	4	124–179 mm	8 Sep 1963	Gulf of Guinea, off Congo
Monomitopus microlepis	USNM 74156 Holotype	1	227 mm	18 Mar 1909	Cebu, Philippines
Monomitopus microlepis	USNM 99051 Paratype	5	93–167 mm	22 Jul 1908	Luzon, Philippines
Monomitopus nigripinnis	USNM 267531	1	180 mm	13 Apr 1892	Bay of Bengal, India
Monomitopus nigripinnis	USNM 330069	1	153 mm	19 Feb 1987	Gulf of Aden, Somalia
Monomitopus pallidus	USNM 74133 Holotype	1	177 mm	3 Jun 1908	Caluya Island, Philippines
Monomitopus pallidus	USNM 99262 Paratype	1	Damaged	3 Mar 1909	Mompog Island, Philippines
Monomitopus pallidus	USNM 99263 Paratype	1	109 mm	31 Mar 1909	Cagayan Island, Philippines
Monomitopus pallidus	USNM 99264 Paratype	1	183 mm	31 Jul 1909	Panaon Island, Philippines

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APPENDIX 1. (Continued)

Species	Museum Voucher	Count	SL	Collection Date	Collection Locality
Monomitopus torvus	USNM 135354 Syntype	1	Damaged	2 Mar 1888	Ecuador
Monomitopus torvus	USNM 150256	1	269 mm	15 Apr 1888	Ecuador
Monomitopus torvus	USNM 422497	1	161 mm	12 Nov 2010	Panama (Pacific)
Monomitopus torvus	USNM 57875	1	105 mm	8 Mar 1891	Panama (Pacific)
Monomitopus vitiazi	NMV A29719-017	1	120 mm	3 Jul 2007	Northwestern Australia
Monomitopus vitiazi	NMV A29720-009	1	197 mm	3 Jul 2007	Northwestern Australia
Monomitopus vitiazi	NMV A29720-010	2	96–101 mm	3 Jul 2007	Northwestern Australia