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A description of three new bathyteuthid squid species from the North Atlantic and Gulf of Mexico --Manuscript Draft--

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A description of three new bathyteuthid squid species from the North Atlantic and Gulf of Mexico

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Running title: *Bathyteuthis* in the North Atlantic

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Abstract:

Currently, three species in the squid family Bathyteuthidae are recognized as valid: *Bathyteuthis abyssicola* Hoyle 1885, *Bathyteuthis bacidifera* Roper 1968, and *Bathyteuthis berryi* Roper 1968. Using morphology and DNA sequencing (COI, 16S), we discovered three additional species of bathyteuthids collected from the North Atlantic Ocean and adjacent basins between 2009 and 2018. Two of the newly discovered species share the absence of arm-base photophores as well as differences in arm-sucker and buccal-lappet sucker counts. In the third species, the adult female individual has arm-base photophores but the two juveniles (sex undetermined) do not. All examined individuals of this species exhibited <1% divergence rate for the COI locus. We describe and name the three new species based on both morphological and molecular characters.

31 Introduction

32 Currently, three species from the squid family Bathyteuthidae are recognized as valid:

33 *Bathyteuthis abyssicola* Hoyle 1885, *Bathyteuthis bacidifera* Roper 1968, and *Bathyteuthis*

34 *berryi* Roper 1968. These species share a deep reddish-maroon pigmentation, short arms, small,

35 rounded and separated fins, and a small photophore embedded in the base of each arm I-III.

36 These animals inhabit the lower mesopelagic and upper bathypelagic zones and occur throughout

37 the world's oceans (Roper 2012), staying below 600m, and can found as deep as 2000m (Roper

38 1969; Roper and Young 1975). Past research documented these animals as diel vertical

39 migrators in the eastern tropical-subtropical North Atlantic (Clarke and Lu 1975, Lu and Clarke

40 1975) but recent findings indicate other patterns elsewhere (Judkins and Vecchione in prep).

41 Bathyteuthids have been documented in the North Atlantic Ocean in multiple regions: near Bear

42 Seamount off New England (Shea et al. 2017), off Nova Scotia (Vecchione and Pohle 2002),

43 along the northern Mid-Atlantic Ridge (Vecchione et al. 2010), and in the subtropical eastern

44 Atlantic Ocean (Diekman et al. 2002).

45 Other than reports of distribution and abundance, little comprehensive information regarding the

46 life history or biology of bathyteuthids has been published since the monographic work of Roper

47 (1968, 1969). Recently the ammonium content and buoyancy of *Bathyteuthis berryi* was

48 examined by Seibel et al. (2004), who found that, unlike other cephalopods that rely largely on

49 ammonium for flotation, the tissue of *B. berryi* contained little ammonium and larger quantities

50 of an unidentified cation and may use large volume of oil. A few sightings of bathyteuthids

51 using an ROV in the Monterey Canyon area provided new insight into ink utilization (Bush &

52 Robison 2007) and brooding (Bush et al. 2012). Sajikumar et al. (2018) reported age and growth

53 patterns and a range extension of *Bathyteuthis bacidifera* in the Arabian Sea. Attempts to

document the vertical distribution of this family include Roper and Young (1975), Clarke and Lu (1975), and Young (1978) which, when merged, show the bathyteuthids to be a deep-sea squid living in the meso- and bathypelagic zones. Young (1972) described the large extraocular photoreceptors of *Bathyteuthis* located adjacent to the posterior end of each eye. Their beaks and the relationship of beaks with body size were also described by Clarke (1986) and Xavier & Cherel 2009. Bathyteuthids are prey of bottlenose whales (Clarke and Goodall 1994; Sekiguchi et al. 1993).

The collection of morphologically unusual specimens from central and northwestern North Atlantic led to identification of a potential new species, identified as *Bathyteuthis* “sp. A” by Vecchione et al. (2010), in addition to the supposedly widely distributed *B. abyssicola* in the Atlantic Ocean. As part of a multi-gene phylogeny of Decapodiformes, Lindgren (2010) included two *Bathyteuthis* tissue samples: *B. “abyssicola”* and “sp. A,” both of which were collected near Bear Seamount in the northwestern Atlantic Ocean. Although found to be genetically and morphologically distinct from known species, no formal description of “sp. A” was conducted at that time due to a lack of voucher specimens (Fig. 1).

Recently, two comprehensive deep-sea research programs in the Gulf of Mexico (GOM), the Offshore Nekton Sampling and Acoustics Program (ONSAP) and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico program (DEEPEND) collected over 12,500 midwater cephalopods. Among those collected included 51 bathyteuthid specimens, several of which appeared to be morphologically distinguishable from all known species, including the purported “sp.A” from Vecchione et al. (2010). Newly collected material from these GOM cruises and additional material from the eastern North Atlantic now allows for the formal description of three new species based on morphological and molecular characters: “sp. A” which has a range

extending through the entire North Atlantic and two additional bathyteuthids in the Gulf of Mexico (GOM), originally referred to as “sp. B” and “sp. C” (Judkins, unpublished).

Materials and methods

All research cruises used either a 10m² Multiple Opening and Closing Net and Environmental Sensing System (MOC10) or a large midwater trawl for collection (Judkins et al. 2016, Shea et al. 2017, Olivar et al. 2017). After collection, specimens were examined and then preserved in 10% formalin. A tissue sample from each individual was preserved in RNAlater or EtOH. GOM material obtained from the ONSAP Program are labeled with PS and the DEEPEND samples are labeled DP while ICMC refers to the Biological Reference Collections (CBR) of the Institut de Ciències del Mar. Specimens examined are deposited in the following repositories: USNM (National Museum of Natural History, Smithsonian Institution, Washington DC USA) and ICMC (Instituto de Ciencias del Mar, Barcelona, Spain). Of the 51 bathyteuthid specimens examined, ten of thirteen preserved individuals representing the three distinct species groups were successfully analyzed for genetic data (Table 1) and the remaining 36 specimens are preserved in 50% isopropanol (no tissue samples taken) and located at the Judkins Invertebrate Laboratory in St. Petersburg, FL.

Morphological examination

The following measurements and counts were recorded for all specimens: mantle length (ML), arm length (AI, AII, AIII, AIV), tentacle length (TnL), club length (CL), sucker count for each arm, club-sucker count, buccal-lappet count, buccal-lappet sucker count for each lappet, arm sucker dentition, and presence/absence of photophores at the dorsal arm bases. These characters are consistent with past bathyteuthid descriptions (Roper 1969). Length characters were

measured with calipers to the nearest 0.1mm. Measurements of characters that are considered to be bilaterally symmetrical across the midline of the squid were taken from the most intact side of the specimen. A representative external photo of each species is included (Figs. 2, 4, 6). A spatial distribution map including all three species was created using the ArcGIS mapping program (ESRI 2011) (Fig. 8).

Genetic Analysis

Thirteen fresh samples of bathyteuthid tissues were fixed immediately in either 95% EtOH or RNAlater and then frozen until processing. DNA was successfully extracted using the DNeasy Tissue Kit (Qiagen, Valencia CA) from mantle tissue of nine individuals, representing 2-5 samples for each of the three presumed new-species groups. PCR amplifications were carried out in 25µL reaction volumes using the GoTaq Green Master Mix (Promega) with 5ng DNA, 12.5 µL Master Mix and 0.4 µM of each primer. To aid in species-level identification, two molecular loci were amplified: cytochrome oxidase subunit *I* (COI) and 16S rRNA. Primer sequences for both loci were taken directly from the literature (e.g. Lindgren 2010). Standard cycling parameters included a 2 min. hot start at 95°C followed by 30 cycles of 95°C (30 seconds), 38-42°C (30 seconds) and 72°C (45 seconds), with an additional 7 min. elongation period (72°C) prior to refrigeration. All PCR products were checked via gel electrophoresis and with a Qubit v.3 fluorometer (ThermoFisher).

Unpurified PCR products were sent to Genewiz (South Plainfield, New Jersey) for sequencing and the resulting sequences were edited and assembled in Geneious v. 10.0.9. For both COI and 16S, primers were removed from consensus sequences prior to downstream processing. Sequences were aligned using the “Geneious Alignment” algorithm. For the protein-coding COI gene, no length difference exists, so the alignment step was used to check for

erroneous insertion/deletion events. All COI consensus sequences were also translated to check for erroneous internal stop codons. Sequence divergence rates within and among species were calculated using known reference sequences in Geneious v. 10.0.9 (Table 3).

Results

A complete list of specimens examined in these descriptions can be found in Table 1. Appendix 1 contains the complete list of measurements for all three species described below. Both morphological and molecular data recovered three distinct species groups, which are described below. Morphological differences include: arm sucker and buccal lappet sucker counts and the absence of arm photophores in two of the species examined (*B. inopinatum*, *B. devoleii*) (Table 2). Analysis of genetic data (Table 3) revealed that two of the new species, *Bathyteuthis inopinatum* (formerly *Bathyteuthis* sp. A) and *B. numerosus* (*Bathyteuthis* sp. C) each had a 5-7% difference in COI when compared to sequence data for all known species while the third species, *B. devoleii* (formerly *Bathyteuthis* sp. B) exhibited the highest divergence rates: 10-11% for COI and 7-8% for 16S. Individuals within each of the three species groups showed intraspecific divergence rates of less than 1% for both 16S and COI loci.

Systematics

Family Bathyteuthidae Pfeffer, 1900

Monogeneric. Diagnosis as in the genus.

Genus *Bathyteuthis* Hoyle, 1885

Mantle short and continuously dark maroon in color. Fins small, short, round, with free anterior and posterior lobes, subterminal, and without muscular ribs. Fin length approximately 15% of ML. Mantle funnel-locking mechanism straight and simple. Eyes directed anteriorly. Arms are

short with two, increasing to more than two series of numerous, small suckers. Club is short and unexpanded. Buccal connectives attach DDVD. Buccal lappets with small suckers. Suprafunnel pore present.

***Bathyteuthis inopinatum* new species**

Diagnosis. A bathyteuthid without photophores at the bases of arms I-III; arms short (~29% ML) with long tentacles (~3.5x ML), numerous arm suckers (120-190 per arm in squid larger than 35mm ML), the number of buccal lappet suckers (0-5 suckers per individual) varied among specimens examined (Table 2).

Type material.- Holotype, ICMC000156, male, 28 mm ML; NE Atlantic, near Cape Verde Islands; 700-800 m; 10°48'N, 22°40'W; April 19, 2015.

Paratype: ICMC000157; unsexed specimen, 12 mm ML; NE Atlantic, near Cape Verde Islands; 0-800 m; 11°01'N, 22°38'W; April 19, 2015.

Additional material. PS3974, male, 39 mm ML, September 2011; PS3995, female, 48 mm ML, September, 2011; PS3957, female, 55 mm ML, September, 2011 (Table 1).

Partial synonymy. – *Bathyteuthis* sp. A of Vecchione et al. (2010) and Shea et al. (2017).

Probably *Bathyteuthis abyssicola* of Vecchione and Pohle (2002).

Description.— Funnel extends nearly to posterior edge of eye. Anterior funnel opening narrow (24% of funnel length). Head short (32% ML, holotype) and wide with large circular eyes directed anteriorly. Arms short and blunt with no photophores at bases of arms I-III (Table 2). Arm formula is 1, 4 < 2, 3 in length. No trabeculae, protective membrane, or keels on any arms. Webbing between the arms minimal. Arm suckers numerous, averaging 120-190 per arm in

169 squid larger than 35 mm ML;; all approximately 1 mm in diameter. Arm suckers arranged
170 biserially at arm base, gradually becoming clustered towards each arm tip (Fig. 3). Teeth on arm
171 suckers are pointed, 12-14 circling entire inner ring. Tentacles long and thin but broken off
172 before the club on the holo- and paratype (see Remarks). Buccal-connective attachments
173 DDVV. Suckers on buccal lappets range from 0-5 per lappet (varies by individual). Appendix 1
174 includes measurements for the five individuals.

175 Distribution: North Atlantic Ocean and Gulf of Mexico

176 Etymology.—The species name is Latin for “unexpected”. *Bathyteuthis inopinatum* is named for
177 the unexpected finding of this species in the Northwestern Atlantic Ocean and the Gulf of
178 Mexico when the only species reported from those areas was *B. abyssicola*.

179 Remarks

180 Three Gulf of Mexico (GOM) specimens are morphologically identical to the Atlantic Ocean
181 holotype, but genetic sequencing attempts were not successful. One of the specimens listed as
182 additional material (PS3974) did possess intact tentacles (39mm ML, tentacles 3.5x ML) and
183 tentacle clubs (38% ML). There were ~350-400 suckers per club on this specimen.

184

185 ***Bathyteuthis devoleii* new species**

186 Diagnosis. A bathyteuthid without photophores at the bases of arms I-III; short arms (~25%
187 ML) with long tentacles (~1.3x ML), few arm suckers (<100 on 16 mm holotype) and 0-3
188 suckers on buccal lappets (differs among individuals) (Fig. 5) (Table 2). A table of
189 measurements for all documented material is in Appendix 1.

190 Type material.- Holotype: USNM1550571, DP0788, female, 16 mm ML; northern Gulf of
191 Mexico; 1000-1200 m; 26.59°N -86.3°W; May 7, 2016;

192 Paratype: USNM1550572, DP0023, male, 14 mm ML; northern Gulf of Mexico; 1000-1200 m;
193 28°N -88°W; May 6, 2015.

194 Other material examined.—DP0804, female, 10 mm ML, 27.45°N 86.98°W, August, 2015;
195 DP3061, female, 17mm ML, 28.53°N 87.5°W, August 2018; ICMC000158; unsexed, 10 mm
196 ML, NE Atlantic, near Cape Verde Islands; 10°48'N, 22°40'W, April 19, 2015.

197

198 Description.— Funnel is 6.4 mm long and 4 mm wide (anterior) (holotype). Funnel opening is
199 narrow. Head is short (avg. 7 mm, all material examined) and wide with large eyes. Arms are
200 short (~25% ML) and conical with no photophores present at the bases of arms I-III. Subtle,
201 wavy trabeculae present on arms. Webbing between arms is minimal. Few arm suckers,
202 averaging 73 per arm and averaging 1 mm in diameter. Arm suckers arranged biserially at the
203 base, gradually becoming tightly grouped without clear organization towards arm tip (Fig. 5).
204 Teeth of the arm suckers are truncated; 14-16 per inner sucker ring. Tentacles long (~1.3x ML)
205 and thin. The tentacle club is approximately 18% ML of the holotype. Approximately 400
206 minute suckers on each club. Buccal connectives attach DDVV. Suckers on the buccal lappets
207 0-3 per lappet (varies among individuals).

208 Known distribution: northern Gulf of Mexico and tropical eastern North Atlantic

209 Etymology.— *Bathyteuthis devoleii* is named after George C. Devol, an American inventor who
210 is credited with being the “Father of Robotics” because he invented the robotic arm in 1954
211 which transformed the automotive manufacturing industry. The “Devol” squid honors the
212 grandfather of H. Judkins.

213 Remarks

This species is the smallest of the bathyteuthids that has been examined in this study; the five specimens range from 10-17 mm ML. They appear to be juveniles; although the adult size is unknown, we suspect this will prove to be a dwarf species. The distributional range for this species is the GOM to, at least the tropical eastern North Atlantic.

***Bathyteuthis numerosus* new species**

Diagnosis. A bathyteuthid with photophores at the bases of arms I-III of some individuals (Holotype, Paratype #1); no photophores on the arms of Paratype #2; long, attenuate arms (~48% ML), and 5-7 suckers on buccal lappets, varying individuals (Table 2). Appendix 1 contains all measurements for examined material.

Type material.- Holotype: USNM 1422121, HB_2009_02_STA30_04July; female, 44 mm ML, Mid-Atlantic Ridge; 53.02°N 33.6°W; July 4, 2009.

Paratype #1: USNM1550574; DP0015, juvenile, sex undetermined, 23 mm ML; northern Gulf of Mexico; 1200-1500 m; 29°N 87.5°W; May 3, 2015.

Paratype #2: USNM1550575; DP9096, juvenile, sex undetermined, 20 mm ML; northern Gulf of Mexico; 1200-1500 m; 27.01°N 87.51°W; August, 2016.

Description.— Anterior funnel opening is 4mm wide (holotype). Head is short (26% ML holotype) and wide with large eyes. The arms are long and attenuate (~48% ML) with photophores present at the bases of arms I-III on the adult female holotype and paratype #1 (juvenile). Paratype #2 (juvenile) does not possess arm-base photophores. There are slight, wavy trabeculae on arms, not as thick as trabeculae of *B. devoleii*. Minimal webbing between arms. All arms appear to be same length (vary by 1-2mm maximum) (Appendix 1). Arm suckers

extremely numerous, averaging 164 per arm and averaging 1 mm in diameter. Arm suckers are arranged biserially at the base gradually increasing to a dense, unorganized pattern towards arm tip (Fig. 7). Teeth of the arm suckers are truncate with eight teeth per inner sucker ring.

Tentacles are long and thin but broken off before the club. Buccal connective attachments are DDVV. Suckers on the buccal lappets range from 5-7 per lappet (varies among individuals).

Distribution: Northwestern Atlantic Ocean and the northern Gulf of Mexico

Etymology.—The name translated from Latin means “numerous”. *Bathyteuthis numerosus* is named for the extremely abundant arm suckers found on individuals of this species.

Remarks

This species was found in two distinct localities. The holotype was collected from the northern Mid-Atlantic Ridge, while the paratypes were caught in the northern GOM. While the holotype and paratypes are genetically identical, they possess differences in the presence/absence of arm photophores. Two specimens (holotype (female) and paratype 1 (juvenile)) possess arm-base photophores. Paratype #2 is also a juvenile and does not possess arm photophores. This difference in presence/absence of photophores may be a dimorphic trait. Another possibility is that since the two juveniles are only 3mm apart in ML, this is the size at which photophores first develop for this species. Additional adult male and female material is required to reconcile this observation.

Discussion

The discovery of three new species of deep-sea squid is not surprising based on the little deep-pelagic sampling effort to date, particularly for genetic data (Robison 2009, Webb et al. 2010). An example of this is in the GOM, where only one marine mammal survey had systematically

260 collected deep-sea cephalopods for examination and documentation prior to the Deepwater
261 Horizon oil spill (Judkins et al. 2013). Deep-sea regions are currently undergoing concentrated
262 sampling efforts and continue to reveal new species (DEEPEND, 2017). Recent research efforts
263 in the GOM such as the ONSAP and the DEEPEND programs are the most comprehensive
264 surveys to date for the deep-water column in this region (Judkins et al. 2016). There are sure to
265 be additional new discoveries as exploration continues in the deep-water column (Ramirez-
266 Llorde et al. 2010).

267 This study doubles the number of known species for a poorly-known lineage of cephalopods
268 raising several questions regarding the overall evolution and taxonomy of Bathyteuthidae. A
269 taxonomic review of the family is underway which will shed light on the evolutionary
270 relationships among all species with specific focus on testing the hypothesis that *B. abyssicola* is
271 truly a cosmopolitan species.

272

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284

285

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Table 1. List of bathyteuthid material included for species descriptions.

Species	Voucher #	ML (mm)	Genetics	Ship	Location	Station	Date	Net Type	Depth (m)	Genbank Accession# (COI)	Genbank Accession# (16S)
<i>Bathyteuthis inopinatum</i>	PS3995	48	N	Pisces	GoM	MTSW5DD	24 Sept 2011	Trawl	1400		
<i>Bathyteuthis inopinatum</i>	PS3957	55	N	Pisces	GoM	MTB082DN	11 Sept 2011	Trawl	1400		
<i>Bathyteuthis inopinatum</i>	PS3974	39	N	Pisces	GoM	MTSW7DD	21 Sept 2011	Trawl	1400		
<i>Bathyteuthis inopinatum</i>	ICMC000156	28	16S, COI	Hesperides	NE Atlantic	PEL08D	19April 2015	Midwater trawl	700-800	MN136202	MN136211
<i>Bathyteuthis inopinatum</i>	ICMC000157	12	16S, COI	Hesperides	NE Atlantic	PEL08N	19April2015	Midwater trawl	0-800	MN136203	MN136210
<i>Bathyteuthis devoleii</i>	ICMC000158	10		Hesperides	NE Atlantic	PEL08D	19April 15	Midwater trawl	700-800	n/a	MN136218
<i>Bathyteuthis devoleii</i>	DP0804	10	16S, COI	Point Sur	GoM	BO79N	18Aug15	MOC10	1000-1200	MN136207	MN136215
<i>Bathyteuthis devoleii</i>	DP0788	16	16S, COI	Point Sur	GoM	SE-4N	07May16	MOC10	1000-1200	MN136206	MN136214
<i>Bathyteuthis devoleii</i>	DP0023	14	16S, COI	Point Sur	GoM	B082N	06May15	MOC10	1000-1200	MN136205	MN136213
<i>Bathyteuthis devoleii</i>	DP3061	17	16S	Point Sur	GoM	B252N	30July18	MOC10	1000-1200	n/a	MN136216
<i>Bathyteuthis numerosus</i>	DP0015	23	16S, COI	Point Sur	GoM	B175D	03May15	MOC10	1200-1500	MN136204	MN136212
<i>Bathyteuthis numerosus</i>	USNM 1422121	44	16S	Bigelow	Mid-Atlantic Ridge	30	04July2009	Trawl		n/a	MN136217
<i>Bathyteuthis numerosus</i>	DP9096	20	COI	Point Sur	GoM	SE-2N	10Aug16	MOC10	1200-1500	MN136209	n/a

Table 2. *Bathyteuthis* species comparison

Character	<i>B. abyssicola</i>	<i>B. bacidifera</i>	<i>B. berryi</i>	<i>B. inopinatum</i> (sp. A)	<i>B. devoleii</i> (sp. B)	<i>B. numerosus</i> (sp. C)
Arm base photophores	present	present	present	absent	absent	Present (males) Absent (females)
Protective membranes	present	Reduced or absent	Well developed	absent	absent	Reduced or absent
Trabeculae	None	Free, fleshy, elongate	None	None	Short and fleshy	Slight and wavy
Arm Suckers	Few (100) (I-III)	Numerous (150) (I-III)	Abundant (275) (I-III)	Numerous (40-90 small specimens; 120-190 larger specimens)	Few (<100 arms I-III)	Extremely abundant (150-350) size dependent
Sucker ring dentition (arms)	8-18, bluntly rounded to truncate	18-34, tightly packed and truncate	10-14, small, rounded or subtriangular	12-14, truncate	13-15; truncate	26-24; truncate
Arms	Short, blunt	Short, blunt	Long, attenuate	Short, blunt	Short, blunt	Long, attenuate
Tentacles and clubs	Both relatively short	long	Long tentacles with short clubs	Long	Long; clubs distal ¼ of tentacle (DP0788)	Long; no clubs on holotype
Buccal lappet suckers	0-3	Not available	4-6	0-5	0-3	5-7
Geographic Region	Bear Seamount; Gulf of Mexico	Pacific Ocean	Pacific Ocean	North Atlantic Ocean (and Gulf of Mexico based on morphology)	Gulf of Mexico	Gulf of Mexico and northwestern Atlantic Ocean

Sources 1st 3 columns: Roper 1969, Roper www.tolweb.org: 2007, 2012, 2013, 2014. Current descriptions for new species= this paper.

Table 3. % Sequence similarity for COI and 16S (respectively) across Bathyteuthidae.

	<i>B. abyssicola</i> COI: AF000030 16S: EU735199	<i>B. bacidifera</i> COI: KX905137 16S: n/a	<i>B. berryi</i> COI: AY616886 16S: AY616878	<i>B. inopinatum</i> (sp. A)	<i>B. devoleii</i> (sp. B)
<i>B. inopinatum</i> (sp. A)	95% 99%	93% n/a	95% 99%		
<i>B. devoleii</i> (sp. B)	89% 93%	90% n/a	89% 92%	90% 92%	
<i>B. numerousus</i> (sp. C)	94% 99%	93% n/a	94% 99%	95% 98%	89% 85%

Figures:

Figure 1. *Bathyteuthis* sp. A from Bear Seamount area showing lack of photophores at the arm bases (Image: M. Vecchione)

Figure 2. Dorsal, lateral and ventral view of *Bathyteuthis inopinatum*. Holotype, male 28 mm ML (image courtesy of VM Tuset)

Figure 3. *B. inopinatum*. A. dorsal view, no photophores at arm bases; B. arm suckers; C. buccal lappet suckers (Image: P. Nolan).

Figure 4. Dorsal view of *Bathyteuthis devoleii* (photo: D. Fenolio)

Figure 5. *B. devoleii*; A. lack of arm-base photophores; B. arm suckers; C. buccal lappet suckers (holotype); D. buccal lappet suckers (paratype). (Image: P. Nolan)

Figure 6. Lateral view of *Bathyteuthis numerosus* (photo: D. Fenolio)

Figure 7. *B. numerosus*; A. no arm photophores (paratype 2); B. arm photophores (holotype, paratype 1); C. arm suckers; D. buccal lappet suckers (holotype); E. buccal lappet suckers (paratype 2) (Image: P. Nolan).

Figure 8. Spatial distribution of the three bathyteuthid species in the North Atlantic.

<i>Bathyteuthis inopinatum</i>		2 NIVEL 1 PELO8 DIA	3 PEL08 NIVEL 1 DIA	PS3974	PS3995	PS3957
Cruise / Date		PELO8; northwestern Atlantic	PELO8; northwestern Atlantic	NRDA PC12 / 09/11	NRDA PC12 / 09/11	NRDA PC12 / 09/12
Original ID		Bathyteuthis sp.	Bathyteuthis sp.	Bathyteuthis sp. A	Bathyteuthis sp. A	Bathyteuthis sp. A
Confirmed ID		<i>Bathyteuthis inopinatum</i> - HOLOTYPE	<i>Bathyteuthis inopinatum</i> - PARATYPE	<i>Bathyteuthis inopinatum</i>	<i>Bathyteuthis inopinatum</i>	<i>Bathyteuthis inopinatum</i>
Mantle Length (mm)	ML	28	12	39	48	55
Sex	M/F	male	Unknown	M	F	F
Arm Photophores		None	None	None	None	None
Trabeculae	Y/N	None	unknown	None	None	None
Arm, Tent, Club L (mm)	L1	7	4	14	21	14
	L2	7	5	13	24	17
	L3	8	5	14	24	18
	L4	8	5	20	25	18
	R4	8	5	21	26	17
	R3	8	5	20	23	17
	R2	7	4	16	21	17
	R1	7	4	13	22	16
	LT	13 (damaged)	missing	136	missing	missing
	RT	25 (damaged)	missing	134	missing	missing
	LC	missing	missing	14	missing	missing
	RC	missing	missing	15	missing	missing
Arms, Clubs Sucker Count	L1	89	45	132	160	170
	L2	81	58	140	168	185
	L3	85	damaged	145	175	195
	L4	85	damaged	148	176	191
	R4	79	damaged	135	173	183
	R3	83	52	135	169	178
	R2	84	47	120	165	179
	R1	86	damaged	122	154	180
Left Club Sucker Ct	LC	missing	missing	~350	missing	missing
Right Club Sucker Ct	RC	missing	missing	~400	missing	missing
Sucker Ring Dentation (near base)	Type	pointed; 12-14	pointed	pointed	pointed	pointed
	Arm: #	RIII		L1	L1	R1
Sucker Count on Buccal Lappets	# lappets	7	7	8	8	9
	Lappet attachment	DDVD	n/a	DDVD	DDVD	DDVD
	# Suckers per lappet	3	3	4	3	3

<i>Bathyteuthis devoleii</i>		DP0788	1 Integrada PELO8 NOCHE	DP0804	DP3061	DP0023
Cruise / Date		DP03; 05/2016	PELO8; northwestern Atlantic	DP02; 08/2015	DP06, 08/2018	DP01; 05/2015
Original ID		<i>Bathyteuthis</i> sp.	<i>Bathyteuthis</i> sp.	<i>Bathyteuthis</i> sp. A	<i>Bathyteuthis</i> sp. A	<i>Bathyteuthis</i> sp. A
Confirmed ID		<i>Bathyteuthis devoleii</i> - HOLOTYPE	<i>Bathyteuthis devoleii</i> - PARATYPE	<i>Bathyteuthis devoleii</i>	<i>Bathyteuthis devoleii</i>	<i>Bathyteuthis devoleii</i>
Mantle Length (mm)	ML	16	9	10	17	10
Sex	M/F	F	unknown	F	F	M
Arm Photophores		none	none	none	none	none
Trabeculae	Y/N	wavy	none	wavy	wavy	wavy
Arm, Tentacles, Clubs Lengths (mm)	L1	4	4	missing tip	6	4
	L2	4	5	missing tip	missing	4
	L3	4	4	missing tip	6	4
	L4	4	5	5	6	4
	R4	4	5	5	5	4
	R3	4	4	missing tip	5	4
	R2	4	4	missing tip	6	4
	R1	4	4	4	6	4
	LT	21	19 (damaged)	31	missing	missing
	RT	20	missing	missing tip	missing	missing
	LC	3	missing	2	missing	missing
	RC	3	missing	missing tip	missing	missing
Arms and Clubs Sucker Count	L1	73	44	missing tip	60	37
	L2	71	53	missing tip	58	45
	L3	75	51	missing tip	63	42
	L4	80	49	22	55	43
	R4	78	49	27	50	40
	R3	69	51	missing tip	63	41
	R2	75	47	missing tip	60	38
	R1	61	41 (damaged)	25	52	36
Left Club Sucker Ct	LC	~400	missing	missing tip	missing	missing
Right Club Sucker Ct	RC	~400	missing	25	missing	missing
Sucker Ring Dentation (near base)	Type	truncated	truncated	n/a	truncated	truncated
	Arm: #	14-16; L4	L3	all arms	8-10; R4	n/a
	# Lappets	7	7	7	7	6

Sucker Count on Buccal Lappets	# Suckers per Lappets	3	3 (some damage)	2	2	0
	Lappet attach	DDVD	DDVD	DDVD	DDVD	DDVD

<i>Bathyteuthis numerosus</i>		HB2009_02STA30_04JU_USNM#1422121	DP0015	DP9096
Cruise / Date		Bear Seamount	DP01; 05/2015	DP04 ; 08/2016
Original ID		Bathyteuthis sp. A	Bathyteuthis abbyssicola	Bathyteuthis sp. A
Confirmed ID		<i>B. numerosus</i> -HOLOTYPE	<i>B. numerosus</i> PARATYPE 1	<i>B. numerosus</i> Paratype 2
Mantle Length (mm)	ML	44	23	20
Sex	M/F	female	juvenile	juvenile
Arm Photophores		yes	yes	none
Trabeculae	Y/N	slight, wavy	slight, wavy	slight, wavy
Arm, Tentacles, Clubs Lengths (mm)	L1	21	8	3, missing tip
	L2	21	8	5, missing tip
	L3	22	8	6
	L4	23	missing tip	7
	R4	21	missing tip	7
	R3	21	missing tip	4, missing tip
	R2	21	missing tip	4, missing tip
	R1	21	8	3, missing tip
	LT	missing	missing	missing
	RT	missing	missing	missing
	LC	missing	missing	missing
	RC	missing	missing	missing
Arms and Clubs Sucker Count	L1	156	191	87
	L2	148	184	missing tip
	L3	166	199	81
	L4	172	missing tip	missing tip
	R4	162	missing tip	missing tip
	R3	180	missing tip	missing tip
	R2	159	missing tip	78
	R1	165	187	missing tip
Left Club Sucker Ct	LC	missing	missing tip	missing
Right Club Sucker Ct	RC	missing	missing tip	missing
Sucker Ring Dentation (near base)	Type	truncate; 8-10 one side, other side smooth	n/a	truncate, 8 on 1 side, smooth other side
	Arm: #	L2	n/a	R3
Sucker Count on Buccal Lappets	# Lappets	7	7	7
	# Suckers per Lappet	3	2	3
	Lappet attachment	DDVD	DDVD	DDVD

1 **A description of three new bathyteuthid squid species from the North Atlantic and Gulf of**
2 **Mexico**

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15 Running title: Bathyteuthis in the North Atlantic

16 Key Words: cephalopods, squid, phylogenetics, deep-sea, DEEPEND consortium

17

18 Abstract:

19 Currently, three species in the squid family Bathyteuthidae are recognized as valid: *Bathyteuthis*
20 *abyssicola* Hoyle 1885, *Bathyteuthis bacidifera* Roper 1968, and *Bathyteuthis berryi* Roper
21 1968. Using morphology and DNA sequencing (COI, 16S), we discovered three additional
22 species of bathyteuthids collected from the North Atlantic Ocean and adjacent basins between
23 2009 and 2018. Two of the newly discovered species share the absence of arm-base photophores
24 as well as differences in arm-sucker and buccal-lappet sucker counts. In the third species, the
25 adult female individuals ~~[there is only one female]~~ have arm-base photophores but the two
26 juveniles (sex undetermined) do not ~~[only one juvenile—paratype 2—does not]~~. All examined
27 individuals of this species exhibited <1% divergence rate for the COI locus. ~~[these were the two~~
28 ~~GOM juveniles; the only sexed squid had no COI data. The sentence is misleading].~~ We
29 ~~therefore~~ tentatively propose these photophores may be a sexually dimorphic trait for the ~~third~~
30 ~~species, but more adult males need to be examined to verify this hypothesis. [Your hypothesis is~~
31 ~~too weakly supported to include in the abstract].~~ We describe and name the three new species
32 based on both morphological and molecular characters.

33

34

35 Introduction

36 Currently, three species from the squid family Bathyteuthidae are recognized as valid:

37 *Bathyteuthis abyssicola* Hoyle 1885, *Bathyteuthis bacidifera* Roper 1968, and *Bathyteuthis*
38 *berryi* Roper 1968. These species share a deep reddish-maroon pigmentation, short arms, small,
39 rounded and separated fins, and a small photophore embedded in the base of each arm I-III.

40 These animals inhabit the lower mesopelagic and upper bathypelagic zones and occur throughout

41 the world's oceans (Roper 2012). ~~They are considered non-vertical migrators,~~ staying below

42 600m, and can found as deep as 2000m (Roper 1969; Roper and Young 1975; ~~Judkins unpubl~~

43 ~~data~~). Past research documented these animals as diel vertical migrators in the eastern tropical-

44 subtropical North Atlantic (Clarke and Lu 1975, Lu and Clarke 1975) but recent findings dispute

45 that claim (Judkins and Vecchione in prep). ~~CFER (Tel.) "The population in the eastern tropical-~~

46 ~~subtropical North Atlantic also demonstrates a diel vertical migration (Clarke & Lu, 1975; Lu &~~

47 ~~Clarke, 1975).~~

48

49 Bathyteuthids have been documented in the North Atlantic Ocean in multiple regions: near Bear

50 Seamount off New England (Shea et al. 2017), off Nova Scotia (Vecchione & Pohle 2002), along

51 the northern Mid-Atlantic Ridge (Vecchione et al. 2010), and in the subtropical eastern Atlantic

52 Ocean (Diekman et al. 2002).

53 Other than reports of distribution and abundance, little comprehensive information regarding the

54 life history or ~~species composition~~ biology of bathyteuthids has been published since the

55 monographic work of Roper (1968, 1969). Recently the ammonium content and buoyancy of

56 *Bathyteuthis berryi* was examined by Seibel et al. (2004), who found that, unlike other

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57 cephalopods who rely on largely on ammonium for flotation, the tissue of *B. berryi* contained
58 little ammonium and larger quantities of an unidentified cation and may use large volume of oil.
59 A few sightings of bathyteuthids using an ROV in the Monterey Canyon area provided new
60 insight into ink utilization (Bush & Robison 2007) and brooding (Bush et al. 2012). Sajikumar et
61 al. (2018) reported age and growth patterns and a range extension of *Bathyteuthis bacidifera* in
62 the Arabian Sea. Attempts to document the vertical distribution of this family include Roper and
63 Young (1975), Clarke and Lu (1975), and Young (1978) which, when merged, show the
64 bathyteuthids to be a deep-sea squid living in the meso- and bathypelagic zones. Young (1972)
65 described the large extraocular photoreceptors of *Bathyteuthis* located adjacent to the posterior
66 end of each eye, ~~near the fovea~~ **Squids don't have foveas**. Their beaks and their relationship
67 with body size are also described by Clarke (1986) and Xavier & Cherel 2009. Bathyteuthids are
68 prey of bottlenose whales (Clarke & Goodall 1994; Sekiguchi et al. 1993).

69 As part of a multi-gene phylogeny of Decapodiformes, Lindgren (2010) included two
70 *Bathyteuthis* tissue samples: *B. abyssicola* and “sp. A,” both of which were collected near Bear
71 Seamount in the northwestern Atlantic Ocean. Although genetically different, due to a lack of
72 voucher specimens, no formal description of “sp. A” was conducted at that time.

73 The finding of morphologically unusual specimens from central and northwestern North Atlantic
74 and subsequent analysis of COI and 16S loci spurred the idea that there may be found new
75 species present in addition to the supposedly widely distributed *B. abyssicola* in the Atlantic
76 Ocean, originally identified as *Bathyteuthis* “sp. A” (Vecchione et al. 2010). Additional
77 specimens from the eastern North Atlantic complete this species description with holo- and
78 paratype specimens and extend its known range to the entire North Atlantic.

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79 Recently in the Gulf of Mexico (GOM), two comprehensive deep-sea research programs, the
80 Offshore Nekton Sampling and Acoustics Program (ONSAP) and the Deep Pelagic Nekton
81 Dynamics of the Gulf of Mexico program (DEEPEND), collected over 12,500 midwater
82 cephalopods, including 51 bathyteuthid specimens, several of which appeared to be
83 morphologically distinguishable from all known species. Newly collected material now allows
84 for the formal description of “sp. A” as well as two additional bathyteuthids in the Gulf of
85 Mexico (GOM), originally referred to as “sp. B” and “sp. C” (labeled by H. Judkins). We
86 describe here three new bathyteuthid species from the North Atlantic Ocean and the GOM based
87 on morphological and molecular characters.

88 Materials and methods

89 All research cruises used either a 10m² Multiple Opening and Closing Net and Environmental
90 Sensing System (MOC10) or a large midwater trawl for collection (Judkins et al. 2016, Shea et
91 al. 2017, Olivar et al. 2017). Specimens were collected, examined, and preserved in 10%
92 formalin with a tissue sample from each individual preserved in RNAlater or EtOH (Table 1).
93 GOM material obtained from the ONSAP Program are labeled with PS and the DEEPEND
94 samples are labeled DP. Of the 51 bathyteuthid specimens examined, 135 individuals
95 representing the three distinct species groups were used in this study due to successful molecular
96 sequencing (Table 1) only 13 individuals are listed in Table 1 and in the “Type material” and
97 the “Additional material” and the remaining 36 specimens are preserved (no tissue samples
98 taken) and located at the Judkins Invertebrate Laboratory in St. Petersburg, FL (Table 1).

99 Morphological examination

100 The following measurements and counts were recorded for all specimens: mantle length (ML),
101 arm length (AI, AII, AIII, AIV), tentacle length (TnL), club length (CL), sucker count for each
102 arm, club-sucker count, buccal-lappet count, ~~number of~~ buccal-lappet sucker count for each
103 lappet, arm sucker dentition, ~~Need measurements for largest suckers of arms, tentacles and~~
104 ~~buccal lappets~~ and presence/absence of photophores at the aboral arm bases. These characters
105 are consistent with past bathyteuthid descriptions (Roper 1969). Length characters were
106 measured with calipers to the nearest 0.1mm. Measurements of characters that are considered to
107 be bilaterally symmetrical across the midline of the squid were taken from the most intact side of
108 the specimen. A representative external photo of each species is included (Figs. 1-3). A spatial
109 distribution map was created using the ArcGIS mapping program which includes all three
110 species (ESRI 2011).

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111 Genetic Analysis

112
113 ~~Fifteen~~ ~~[thirteen ??]~~ Thirteen freshly cut bathyteuthid tissues were immediately ~~preserved~~
114 ~~fixed~~ in either 95% EtOH or RNAlater and then frozen until processing. DNA was successfully
115 extracted using the DNeasy Tissue Kit (Qiagen, Valencia CA) from mantle tissue of ~~10~~ nine
116 individuals, representing 2-5 samples for each of the three presumed new-species groups. PCR
117 amplifications were carried out in 25µL reaction volumes using the GoTaq Green Master Mix
118 (Promega) with 5ng DNA, 12.5 µL Master Mix and 0.4 µM of each primer. To aid in species-
119 level identification, two molecular loci were amplified: cytochrome oxidase subunit I COI and
120 16SrRNA. Primer sequences for both loci were taken directly from the literature (e.g. Lindgren
121 2010). Standard cycling parameters included a 2 min. hot start at 95°C followed by 30 cycles of
122 95°C (30 seconds), 38-42°C (30 seconds) and 72°C (45 seconds), with an additional 7 min.

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123 elongation period (72°C) prior to refrigeration. All PCR products were checked via gel
124 electrophoresis and with a Qubit v.3 fluorometer (ThermoFisher).
125 Unpurified PCR products were sent to Genewiz (South Plainfield, New Jersey) for
126 sequencing and the resulting sequences were edited and assembled in Geneious v. 10.0.9. For
127 both COI and 16S, primers were removed from consensus sequences prior to downstream
128 processing. Sequences were aligned using the “Geneious Alignment” algorithm. For the protein-
129 coding COI gene, no length difference exists, so the alignment step was used to check for
130 erroneous insertion/deletion events. All COI consensus sequences were also translated to check
131 for erroneous internal stop codons. Sequence divergence rates within and among species were
132 calculated using known reference sequences in Geneious v. 10.0.9 (Table 2).

133 Results

134 Morphological and molecular data ~~consistently~~ recovered three distinct species groups, which are
135 described below. Morphological differences include: arm sucker and buccal lappet sucker
136 counts and the absence of arm photophores in two of the species examined (*B. inopinatum*, *B.*
137 *devoilei*) (Table 2). Analysis of genetic data (Table 3) revealed that two of the new species,
138 *Bathyteuthis inopinatum* (formerly *Bathyteuthis* sp. A) and *B. numerosus* (*Bathyteuthis* sp. C)
139 each had a 5-7% difference in COI when compared to sequence data for all known species-
140 ~~Interestingly, [everything in science is interesting] and while~~ the third species, *B. devoilei*
141 (formerly *Bathyteuthis* sp. B) ~~exhibited the highest divergence rates: exhibited the highest~~
142 ~~divergence:~~ 10-11% for COI and 7-8% for 16S. ~~Individuals w~~Within each of the three species
143 groups, ~~individuals~~ showed an intraspecific divergence rate of ~~<less than~~ 1% for both 16S and
144 COI loci.

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Commented [A1]: From the reviewer 1:
The genetic data clearly indicate that the authors have three new species of *Bathyteuthis*. However, the authors need to clarify the DNA data for one species, *B. numerosus*. Geographically, this species is held together genetically by "<1%" (line 132 in text) divergence of gene 16S between the holotype and paratype 1. Based on the combined 16S data from these two squid, they diverge from two known species of *Bathyteuthis* by 1% and from *B. inopinatum* by 2%. Clearly, "<1%" does not differ greatly from 1%. For the reader to assess the genetic relationship between the holotype and paratype, their exact divergence (which is not given in the manuscript) should be presented. In addition, the authors should estimate, in the light of the low divergence with most other *Bathyteuthis* at this loci, what the odds are that the genetic data uniting the holotype and paratype 1 is due to chance. The result will be either to bolster confidence in the genetic data or indicate that the relationship depends more heavily on the morphological data

Commented [A2R1]: He misread the paper. <1% was *within* each species, not between species. As stated here, each new species has >5% difference in its COI locus. So the way this is written is sufficient.

146 Systematics

147 Family Bathyteuthidae Pfeffer, 1900

148 Monogeneric. Diagnosis as in the genus.

149 Genus *Bathyteuthis* Hoyle, 1885

150 Mantle short and continuously dark maroon in color. Fins small, short, round, . and paddle like,

151 circular in shape, with free anterior and posterior lobes, and subterminal and without muscular

152 ribs. Fin length approximately 15% of ML. Mantle funnel-locking mechanism straight and

153 simple. Eyes directed anteriorly. Arms are short with two, increasing to more than two rows of

154 numerous, small suckers. Club is short and unexpanded. Buccal lappets with small suckers.

155 What about buccal connectives, tentacle pockets, clubs, eye shape, suprafunnel canal?!

156

157 ***Bathyteuthis inopinatum* new species**

158 Diagnosis. A bathyteuthid without photophores at the bases of arms I-III; short arms (~29%

159 ML) with long tentacles (~3.5x ML), numerous arm suckers (120-190 per arm in larger

160 specimens, squid larger than 35mm ML xxx), and the number of buccal lappet suckers (0-5

161 suckers per individual) varied among examined specimens. on per buccal lappets [??] (Table 2).

162 Type material.- ICMCXXXXX/2019 (Biological Reference Collections (CBR) of the Institut de

163 Ciències del Mar); Holotype, male, 28 mm ML; NE Atlantic, near Cape Verde Islands; 700-800

164 m; 10°48'N, 22°40'W; April 19, 2015.

165 Paratype: ICMCXXXXX/2019; unsexed specimen, 129 mm ML, 12 mm in Table 1; NE

166 Atlantic, near Cape Verde Islands; 0-800 m; 11°01'N, 22°38'W; April 19, 2015.

167 Additional material. PS3974, male, 39 mm ML, September 2011; PS3995, female, 48 mm ML,

168 September, 2011; PS3957, female, 55 mm ML, September, 2011 (Table 1).

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Commented [A3]: Include arm length formula here from excel table for rerv 3

Commented [A4]: Check arm suckers on small vs. large specimens to get a ML range

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169 Partial synonymy. – *Bathyteuthis* sp. A of Vecchione et al. (2010) and Shea et al. (2017).

170 Probably *Bathyteuthis abyssicola* of Vecchione and Pohle (2002).

171

172 Description.— ~~External anatomy:~~ ~~[not needed since there is no “Internal anatomy”]~~ Funnel

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173 extends nearly to posterior edge of eye. Funnel opening narrow (24% of funnel length).

174 ~~[Suprafunnel pore ??]~~ Head short (32% ML9 mm, holotype) ~~[occipital crest and folds ??]~~

175 ~~[Olfactory organ ??]~~ and wide with large ~~circular~~ eyes directed anteriorly. ~~[Eye shape ??, optic~~

176 ~~sinus ??, eye orientation]~~ Arms short and blunt with no photophores at bases of arms I-III (Table

177 2). Arm formula is 1,4 < 2,3 in length. ~~[Arm formula ??]~~ No trabeculae, protective membrane,

178 or keels on any arms. ~~[protective membranes ??, keels /]~~ Webbing between the arms minimal.

179 ~~[Examine this more carefully as Bathyteuthids are among the few squids that have webs]~~ Arm

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180 suckers numerous, averaging 84 per arm ~~(1>3, 4>2, holotype)~~ ~~[Does this mean: (arms I with >~~

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181 ~~arms III, arms IV with > arms II, holotype ?]~~ averaging ~~[This is a statistical term; would “all~~

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182 ~~about” be more appropriate ?]~~ all approximately bout 1 mm in diameter. Arm suckers arranged

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183 biserially at arm base, gradually becoming clustered increasing to clusters ~~[explain “clusters”~~

184 ~~very unusual]~~ towards ~~each arm tip of each arm.~~ Teeth on a Arm suckers are teeth pointed, 12-

185 14 ~~circling around~~ entire ~~[?] per~~ inner sucker ring. Tentacles long and thin but broken off before

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186 the club on the holo- and paratype (see Remarks). Buccal-connective attachments DDVV

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187 ~~[error]~~. Suckers on buccal lappets range from 0-5 per lappet. Appendix 1 includes

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188 measurements for the five individuals. ~~[You need a table showing measurements and counts for~~

189 ~~each individual squid (ie., all 5 squid). This is necessary for the reader to evaluate the variation in~~

190 ~~these numbers against squid size and location and for you to demonstrate that the GoM~~

191 ~~specimens are “morphologically identical” to the holotype]~~

192 Distribution: North Atlantic Ocean and Gulf of Mexico

193 Etymology.—The species name is Latin for “unexpected”. *Bathyteuthis inopinatum* is named for

194 the ~~exciting and~~ unexpected ~~new~~ finding of ~~the first of these~~ this species in the ~~northwestern~~

195 ~~Atlantic region. Northwestern Atlantic Ocean and the~~ Gulf of Mexico.

196 Remarks

197 ~~The finding of morphologically unusual specimens from central and northwestern North Atlantic~~

198 ~~and subsequent analysis of COI and 16S loci spurred the idea that there may be found new~~

199 ~~species present in addition to the supposedly widely distributed *B. abyssicola* in the Atlantic~~

200 ~~Ocean, originally identified as *Bathyteuthis* “sp. A” (Vecchione et al. 2010). Additional~~

201 ~~specimens from the eastern North Atlantic complete this species description with holo- and~~

202 ~~paratype specimens and extend its known range to the entire North Atlantic.]~~ ~~[Place this in the~~

203 ~~Introduction.] Multiple GOM.~~ Three Gulf of Mexico (GOM) specimens are morphologically

204 identical to the ~~Eastern Atlantic Ocean Ocean individuals~~ holotype, ~~[I doubt that the 10 mm~~

205 ~~paratype offers much morphological confirmation]~~ but genetic sequencing attempts were not

206 successful. One of the specimens listed as additional material (~~PS3974~~DP 3974) ~~Is this~~

207 ~~PS3974?~~ did possess intact tentacles (39mm ML, ~~tentacles 3.5x ML~~ tentacles ~3.5x ML) and

208 tentacle clubs (~~38% xx%~~ of ML) ~~[length of tentacles is generally a useless measure]~~. There were

209 ~350-400 suckers per club on this specimen. ~~[This info needs to be in the Description.] Genetic~~

210 ~~sequencing is planned for GOM specimens as material becomes available, [obvious & irrelevant~~

211 ~~to present paper]~~

212

213 *Bathyteuthis devoleii* new species

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214 Diagnosis. A bathyteuthid without photophores at the bases of arms I-III; short arms (~25%
 215 ML) with long tentacles (~1.3x ML), ~~few numerous or FEW?~~ arm suckers (<100 on 16 mm
 216 holotype), ~~[Be more specific]~~ and 0-3 suckers on buccal lappets (differs among individuals).
 217 (Table 2).

218 Type material.- Holotype: USNM 1550571-XXXXXXX, DP0788, female, 16 mm ML; northern
 219 Gulf of Mexico; 1000-1200 m; 26.59°N -86.3°W; May 7, 2016;

220 Paratype: USNM 1550572-XXXXXXX, DP0023, male, 14 mm ML; northern Gulf of Mexico;
 221 1000-1200 m; 28°N -88°W; May 6, 2015.

222 Other material examined.—DP0804, female, 10 mm ML, 27.45°N 86.98°W, August, 2015;
 223 DP3061, female, 17mm ML, 28.53°N 87.5°W, August 2018; ICMCXXXXXX/2019; unsexed, 10
 224 mm ML, NE Atlantic, near Cape Verde Islands; 10°48'N, 22°40'W, April 19, 2015.

225

226 Description.— ~~External anatomy~~: Funnel is 6.4 mm long and 4 mm wide (holotype). Funnel
 227 opening is narrow. Head is short (avg. 7 mm, all material examined) and wide with large eyes.
 228 Arms are short (~25% ML) and conical with no photophores present at the bases of arms I-III.
 229 Subtle, wavy trabeculae present on arms. Webbing between arms is minimal. ~~Few~~Numerous
 230 arm suckers, averaging 73 per arm (~~1>3 & 4>2, holotype~~), ~~[explain]~~ and averaging 1 mm in
 231 diameter. Arm suckers arranged biserially at the base, gradually becoming tightly grouped
 232 without clear organization towards arm tip. Teeth of the arm suckers are truncated; 14-16 per
 233 inner sucker ring. Tentacles long (~1.3x ML) and thin. ~~The t~~Tentacle club is approximately
 234 18% ML of the holotype. one quarter length of the tentacle (holotype) [use % ML].
 235 Approximately 400 minute suckers on each club. Buccal connectives attach DDV, V ~~[error]~~.
 236 Suckers on the buccal lappets 0-3 per lappet (varies among individuals).

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237 Distribution: northern Gulf of Mexico and tropical eastern North Atlantic
238 Etymology.— *Bathyteuthis devoleii* is named after George C. Devol, an American inventor who
239 is credited with being the “Father of Robotics” because he invented the robotic arm in 1954
240 which transformed the automotive manufacturing industry. The “Devol” squid honors the
241 grandfather of H. Judkins.

242 Remarks

243 This species is the smallest of the bathyteuthids that have been examined in this study; ~~with all~~
244 ~~the five specimens examined ranging~~ range from 10-17 mm ML. They appear to be juveniles
245 ~~[Apparently they were easily sexed, and they have the species characteristics; they should be~~
246 ~~called subadults] and may that will grow to a larger size as they mature [obvious]~~ although the
247 adult size is unknown, we suspect this will prove to be a dwarf species. The distributional range
248 for this species ~~appears to include~~ is the GOM ~~as well as~~ to, probably, the tropical eastern North
249 Atlantic.

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251 ***Bathyteuthis numerosus* new species**

252 Diagnosis. A bathyteuthid with photophores on the base of arms I-III of some specimens

253 (Holotype, Paratype #1); no arm photophores on the arms of ~~others (Paratype #2)~~ ~~[there is only~~
254 ~~1 paratype 2]~~ long, attenuate arms (~48% ML), ~~[Can you quantify “attenuate”?]~~ and 5-7 suckers
255 on buccal lappets which vary by individual (Table 2).

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256 Type material.- Holotype: USNM 1422121, HB_2009_02_STA30_04July; female, 44 mm ML,
257 Mid-Atlantic Ridge; 53.02°N 33.6°W; July 4, 2009.

258 Paratype #1: USNM 1550574-XXXXXXX; DP0015, juvenile, sex undetermined, 23 mm ML;
259 northern Gulf of Mexico; 1200-1500 m; 29°N 87.5°W; May 3, 2015.

260 Paratype #2: USNM-~~1550575XXXXXXX~~; DP9096, juvenile, sex undetermined, 20 mm ML;
261 northern Gulf of Mexico; 1200-1500 m; 27.01°N 87.51°W; August, 2016.

262
263 Description.— ~~External anatomy:~~ Funnel opening is 4mm wide (holotype). Head is short-(26%
264 ML holotype)(~~41.5 mm long~~) and wide with large eyes. The arms are long and attenuate (~48%
265 ML) with photophores present at the base of arms I-III on the adult female holotype and

266 ~~p~~Paratype #1 (juvenile). Paratype #2 (juvenile) does not possess arm-base photophores. There
267 are slight, wavy trabeculae on arms. They are not as thick as trabeculae of *B. devoleii*. ~~How~~
268 ~~does this differ from “short and fleshy” in *B. devoleii*?~~ Minimal webbing between arms. All
269 arms appear to be same length (vary by 1-2mm maximum) (Appendix 1). Arm suckers extremely
270 numerous, averaging 164 per arm and averaging 1 mm in diameter. Arm suckers are arranged
271 biserially at the base gradually increasing to a dense, unorganized pattern towards arm tip. Teeth
272 of the arm suckers are truncate with eight teeth per inner sucker ring. Tentacles are long and thin
273 but broken off before the club. Buccal connective attachments are DDV-V-~~error~~. Suckers on
274 the buccal lappets range from 5-7 per lappet (varies among individuals).

275 Distribution: Northwestern Atlantic Ocean and the northern Gulf of Mexico

276 Etymology.—The name translated from Latin means “numerous”. *Bathyteuthis numerosus* is
277 named for the extremely abundant arm suckers found on individuals of this species.

278 Remarks

279 This species ~~is widely distributed~~ was found in two ~~distinct~~widely separated localities ~~in the~~
280 ~~North Atlantic Ocean and the Gulf of Mexico.~~ [The original sentence was misleading (ie “widely
281 distributed” implies that this species occurs throughout this region, which may or may not be
282 true. Also it is redundant with the following sentence] The holotype was collected from the

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283 northern Mid-Atlantic Ridge, while the paratypes were caught in the northern GOM. ~~While An~~
 284 ~~interesting note is that, while~~ the holotype and paratypes ~~match genetically~~ are genetically
 285 identical, they possess differences in the presence/absence of arm photophores. Two specimens
 286 (holotype (female) and paratype 1 (juvenile)) possess arm-base photophores. Paratype #2 is also
 287 a juvenile and does not possess arm photophores. ~~The authors identify the~~ [An adult female is
 288 easy to recognize due to its large nidamental glands and large oviducal glands.] holotype ~~as is an~~
 289 ~~adult female while paratypes~~ are 1 is a juveniles and their sex cannot be determined. Paratype 2
 290 ~~has, they have no arm base photophores and is also a juvenile. Tentatively, this could be a~~
 291 sexually dimorphic trait for this species but adult males will need to be examined to verify this
 292 hypothesis. This difference in presence/absence of photophores may be a dimorphic trait or
 293 pPerhaps, since the two juveniles are only 3mm apart in ML, this is the size that photophores
 294 first develop. Additional adult male and female material is required to reconcile this difference.

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296 Discussion-

297 The discovery of three new species of deep-sea squid is not surprising based on the little deep-
 298 pelagic sampling effort ~~effort~~ to date, particularly for genetic data. ~~of the world's oceans.~~ [Not
 299 sampling but lack of genetics has been the problem]. (Robison 2009, Webb et al. 2010). An
 300 example of this is in the GOM, where one marine mammal survey collected deep-sea
 301 cephalopods for examination and documentation prior to the Deepwater Horizon oil spill
 302 (Judkins et al. 2013). Currently, deep-sea regions are undergoing concentrated sampling efforts
 303 and continue to reveal new species (DEEPEND, 2017). Recent research efforts in the GOM
 304 such as ONSAP and the DEEPEND programs are the most comprehensive surveys to date for

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305 the deep water column in this region (Judkins et al. 2016). There are sure to be additional new
306 discoveries as exploration continues in the deep water column (Ramirez- Llorde et al. 2010).
307 This study doubles the number of known species for a ~~poorly-knownn important~~ lineage of
308 cephalopods. ~~[you imply that some lineages are not important. Why is this lineage important?]~~
309 raising several questions regarding the overall evolution and taxonomy of Bathyteuthidae. A
310 taxonomic review of the family is underway which will shed light on the evolutionary
311 relationships among all species, with specific focus on testing the hypothesis that *B. abyssicola* is
312 ~~truly a truly~~ cosmopolitan species (Fig. 4). ~~[What does Fig. 4 have to do with this sentence?]~~

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318 03. This research was made possible by a grant from The Gulf of Mexico Research
319 Initiative. GOM data are publicly available through the Gulf of Mexico Research
320 Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org>
321 doi: 10.7266/N70P0X3T and doi: 10.7266/N7XP7385. H. Judkins acknowledges the
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323 honor him through one of these species descriptions.

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