

***Duobrachium sparksae* (*incertae sedis* Ctenophora Tentaculata Cydippida): A new genus and species of benthopelagic ctenophore seen at 3,910 m depth off the coast of Puerto Rico**

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Abstract: On April 10, 2015, three individuals of an undescribed species of ctenophore were observed moving just above the seafloor in the Arecibo Amphitheater inside the Guajataca Canyon, north-northwest of Puerto Rico at a depth of approximately 3,900 m. The ctenophore is distinctive; having two prominent tentacle arms, a body that is rectangular when observed laterally along the tentacular plane, and rounded when observed laterally along the stomodeal plane. The tentacle arms each give rise to an extensible tentacle bearing short tentilla of uniform length and distribution. One ctenophore appeared to be anchored to the seafloor by its two long flexible tentacles, as well as by two filaments exiting its oral end. The overall form of the ctenophore suggests classification within the problematic, non-monophyletic order Cydippida, but the robust tentacle arms are more reminiscent of benthic species of Platyctenida, particularly those of families Lyroctenidae and Ctenoplanidae. Whereas most platyctenid ctenophores do not possess ctene rows in their adult forms, features that are possessed by the new species described herein, species of Ctenoplanidae retain comb rows as adults and are capable of limited swimming. The species described herein is easily distinguishable from all other known species of Ctenophora and may trace its origin to a lineage diverging near the origin of Platyctenida.

Key words: Aricebo Amphitheater, Ctenophora, *Duobrachium sparksae* gen nov. & spec. nov., Puerto Rico, Cydippida

Introduction

Ctenophora is perhaps the most enigmatic animal phylum in terms of both evolution and systematics. Its origin within Metazoa has long been shrouded in mystery, giving rise to a lively debate about its phylogenetic origin, which within the past 10 years has been hypothesized as the sister group to Cnidaria (Philippe et al. 2009, Zhao et al. 2019), to all other animals (Whelan et al. 2017, Laumer et al. 2019), and to Placozoa+Cnidaria+Bilateria (Feuda et al. 2017, Simion et al. 2017). At the level of species, ctenophores also pose special challenges for biodiversity

researchers. First, a large portion of the 200 or so accepted species are only encountered at great depths (Haddock 2004) and thus are difficult to collect. And secondly, they are notoriously difficult to preserve for morphological studies (Gershwin et al. 2010), making the creation of morphological vouchers an extreme challenge.

Due to the consequent lack of well-preserved museum specimens allowing for detailed morphological observation, new species are only sporadically described (roughly one species per year; World Registry of Marine Species 2019) and these rely heavily on photographic observations of live material (e.g., Gershwin et al. 2010, Lindsay et al. 2017). Further hindering taxonomic studies of Ctenophora is the lack of the development of a barcode marker, at least

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in part due to the fact that they have highly unusual mitochondrial genomes (Arafat et al. 2018, Wang & Cheng 2019). The moderate accumulation of species (World Registry of Marine Species 2019) stands in contrast to a general appreciation that there is a large number of undescribed species already known by common names (Mills 2019). Estimates for the total richness within Ctenophora are high, with only half or fewer of the existing species having been described (Appeltans et al. 2012, Mills 2019). These taxonomic difficulties pose a problem because ctenophores are important but understudied players in pelagic ecosystems. For example, Harbison et al. (1978) encountered oceanic ctenophores in the majority of their 250 open ocean dives and described them as the “ignored component” of

the open ocean ecosystem since many are never reported in conventional net tows.

On April 10, 2015, three individuals of a remarkable species of ctenophore, not matching any other described species, were observed just above the seafloor at approximately 3,900 m from the Remotely Operated Vehicle (ROV) *Deep Discoverer* during the first dive of the Océano Profundo Expedition (EX1502) of the NOAA Ship *Okeanos Explorer* operating 38 km north-northwest of Puerto Rico (18°51.716'N, 066°48.878'W). The three ctenophores were encountered at separate times during the same dive, each within two meters of the seafloor (Table 1). High definition videos have been cataloged as part of the Smithsonian National Museum of Natural History collections

Table 1. Anatomical features of *Duobrachium sparksae* n. gen. n. sp., with references to observations in type videos¹.

Morphology	Size	Video ref. USNM	Time of Best View	Remarks	Other Observations
Body shape (tent. plane)	6–8 cm	1607331	3:27–3:36	Rectangular in tentacular plane	1607333
Body shape (stom. plane)	6–8 cm	1607332	1:01–1:19	Oblong in stomodeal plane	1607331,-3
Arms	2–3 cm	1607332	1:57–2:40	Two, conical with aboral tentacle openings at vertex	1607331,-3
Marginal furrows	6–8 cm	1607332	2:17–2:37	Two, thin, extend from mouth aborally to tentacle openings on arms	1607331
Ctene rows	2–2.5 cm	1607332	1:09–1:32	Eight, 28 to 32 ctenes per row, extend orally nearly halfway up body	1607331,-3
Mouth	2 cm	1607332	1:09–1:17	Long, slit-like with internal cavity	1607331,-3
Mouth (opening)	2 cm	1607331	1:13–1:23	Opens in tentacular plane, observed gaping centrally (~.25 cm)	none
Tentacle(s) (extended)	30–56 cm	1607331	0:58–1:04	Two, opaque white and evenly thick along entire length	1607332,-3
Tentacle(s) (coiled)	—	1607331	1:17–1:20	Tentacles coil within tentacle sheath	1607333
Tentacle(s) (tension)	30–56 cm	1607332	1:00–4:50	Tentacles under tension, implying attachment to sediment	none
Tentilla	0.5 cm	1607332	1:09–2:40	Numerous, simple, along entire length of tentacle in 4 mm intervals	1607331,-3
Tentacle sheaths	4–6 cm	1607333	0:45–0:52	Wing-shaped in tentacular plane	1607331
Oral filaments		1607332	1:14–2:36	Two, very fine, indicated by aggregated particles extending from oral region down toward seafloor, to which they likely attach	none
Gonads	1 cm	1607332	1:56–2:24	Eight, beneath mid-region of ctene rows, containing eggs/embryos	1607331
Eggs/Embryos	1.5–2.0 mm	1607332	1:56–2:24	Round	none
Gonads (alternative)	1 cm	1607331	3:20–3:36	Eight, located under each ctene row	1607332
Stomodeum (tent. plane)	3–4 cm	1607331	3:27–3:35	Dark-colored, oval in the tentacular plane	1607333
Stomodeum (stom. plane)	3–4 cm	1607331	1:12–1:20	Dark-colored, goblet-shaped in the stomodeal plane	1607332,-3
Meridional canals	1.8–2.3 cm	1607331	0:52–1:03	Eight, slightly shorter than ctene rows	1607332
Adradial canals	—	1607331	0:52–1:03	Presumed to be eight, but not completely visible	none
Apical organ	—	1607332	2:23–2:34	Slightly indented with no visible folds	none

¹ EZID ARK Identifiers are as follows:

USNM 1607331: <http://n2t.net/ark:/65665/38d0e551c-4414-4dfa-b913-e4191f631db0>

USNM 1607332: <http://n2t.net/ark:/65665/32989d925-263c-4d08-875c-15f65f431b40>

USNM 1607333: <http://n2t.net/ark:/65665/3957b35bd-950c-4dc5-8f37-7897ed2f4d03>

under USNM numbers 1607331-3.

Methods

The ROV *Deep Discoverer* encountered these specimens while exploring the seafloor. *Deep Discoverer* is part of a two-body ROV system with a 6000 m endurance that includes *Deep Discoverer* and the camera sled *Seirios*. *Deep Discoverer* measures 3.16×1.96×2.59 meters (length×width×height). Video was recorded with an Insite Pacific “Zeus Plus” HD Video Camera, producing video at a resolution of 1920×1080 pixels, using a frame rate of 29.97i, and the ProRes 442 @ 139 Mbps codec. Lighting was provided by 24 Deepsea Power and Light “Sealite Sphere” LED lamps (144,000 lumens total), and two Deepsea power and Light “LED Multi SeaLite” auxiliary lamps. Color correcting procedures were employed when the cameras reached a stable operating temperature at depth and were held constant throughout the dive. Video Form Monitor and Vector Scope along with a color chip from DSC Labs were used in the procedure to obtain true and unbiased colors in the ROV video. Lasers emit two points 10 cm apart to help scale images. Physicochemical measurements were made with an ROV-mounted SeaBird SBE-911 Plus CTD. Depth and position information was measured using an ROV-mounted Paroscientific 8B7000-I depth sensor and a Tracklink 10000 Ultra Short Baseline (USBL) Acoustic Tracking System.

Results

Phylum Ctenophora Eschscholtz, 1829
 Class Tentaculata Eschscholtz, 1825
 Order Cydippida Gegenbaur, 1856
 Family Cydippida incertae sedis
 Genus *Duobrachium* gen. nov.

Diagnosis. Tentaculate cydippid ctenophores with two thick, aboral, conical tentacle arms. Tentacle arms emerge from the center of the body and extend aborally. Body rectangular in the tentacular plane, oblong in the stomodeal plane. The tentacle arms are as long as the body is tall. Tentacles retractile, with simple tentilla of uniform length. Filaments can exit orally, anchoring it to the sediment. Stomodeum darkly pigmented. Gonads globular, not extending the length of the meridional canals.

Type species. *Duobrachium sparksae* n. sp., described herein.

Etymology. From the Latin “two-arms”, a name reflecting the two prominent arms. The Latin “brachium” is of common gender, but shall be treated as feminine, in accordance with ICZN article 30.1.4.2.

Duobrachium sparksae spec. nov.
 (Figures 1–3, 5)

Material examined. Holotype video, USNM 1607331; two paratype videos, USNM 1607332-3. Collection was

impossible at this location due to vehicle capabilities.

Diagnosis. Same as for genus.

Description. Bodies semi-transparent with two tentacles sheathed in two large conical tentacle arms extending aboral of the body (Table 1). Based on ROV-mounted lasers being 10 cm apart, the estimated length of one specimen (USNM 1607332) from the oral end to the tips of the tentacle arms is 6–8 cm, with the tentacle arms about one-third as long as the body. Lasers were not used to measure the other two animals observed, but contextual scaling objects suggest they were similar in size to the laser-measured animal. Body forms roughly rectangular as viewed laterally in the tentacular plane, but a more oblong rounded shape in the stomodeal plane (Figs. 1–3). Stomodeum dark-colored, oval in shape when viewed from the tentacular plane and goblet-shaped on the stomodeal plane (Figs. 1–3). Eight ctene rows, consisting of 28 to 32 combs per row as counted in the high-definition video, ascend from the apical organ approximately halfway to the oral end, originating from the apical organ unbranched (Fig. 2C). At the oral end, opposite the apical organ, an irregularly undulating bright line with a visible cavity is interpreted as a wide mouth (Fig. 1A, Fig. 2B). Blue to white-colored gonads (eight in total) located under each of the eight ctene rows near their oral ends, presumably within meridional canals (Fig. 1–3), which cannot be directly discerned through the high definition videos. Gonads contain distinct round bodies, eggs or embryos, estimated to be 1.5–2.0 mm in diameter (Figs. 1C, D, 2A, 3).

Tentacle arms encase retractile tentacles within tentacle sheaths (Figs. 1–3). Tentacles thick, opaque white, estimated to be five to seven times the length of the body (including tentacle arms), or approximately 30–56 cm, and appear to be capable of adhering to the seafloor. Tentacles are tentilla-bearing and originate from a tentacle bulb near the stomodeum. Tentilla are simple, uniform, approximately 0.5 cm in length, regularly-spaced at roughly 4 mm intervals along extended tentacles. When retracted, tentacles form a coil inside the translucent tentacle sheath and just outside the tentacle arm (Fig. 1A, 3A). Tentacle sheaths form a wing-like shape that connects to the stomodeum right above the gonads (Fig. 2A). Two fine filaments extend from the oral end of the body (Fig. 5.)

Etymology. The specific epithet “sparksae” honors Elizabeth Ann Sparks, the wife of Michael Ford.

Common name. Sparks’ two-armed ctenophore.

Distribution. Only known from Guajataca Canyon, north-northwest of Puerto Rico at a depth of approximately 3,900 m, within meters of the seafloor.

Electronic Registration: This published work and the nomenclatural acts it contains have been registered in ZooBank under LSID: urn:lsid:zoobank.org:pub:B1BD0C96-F9A8-47A0-BA3F-F42A32B4B91D.

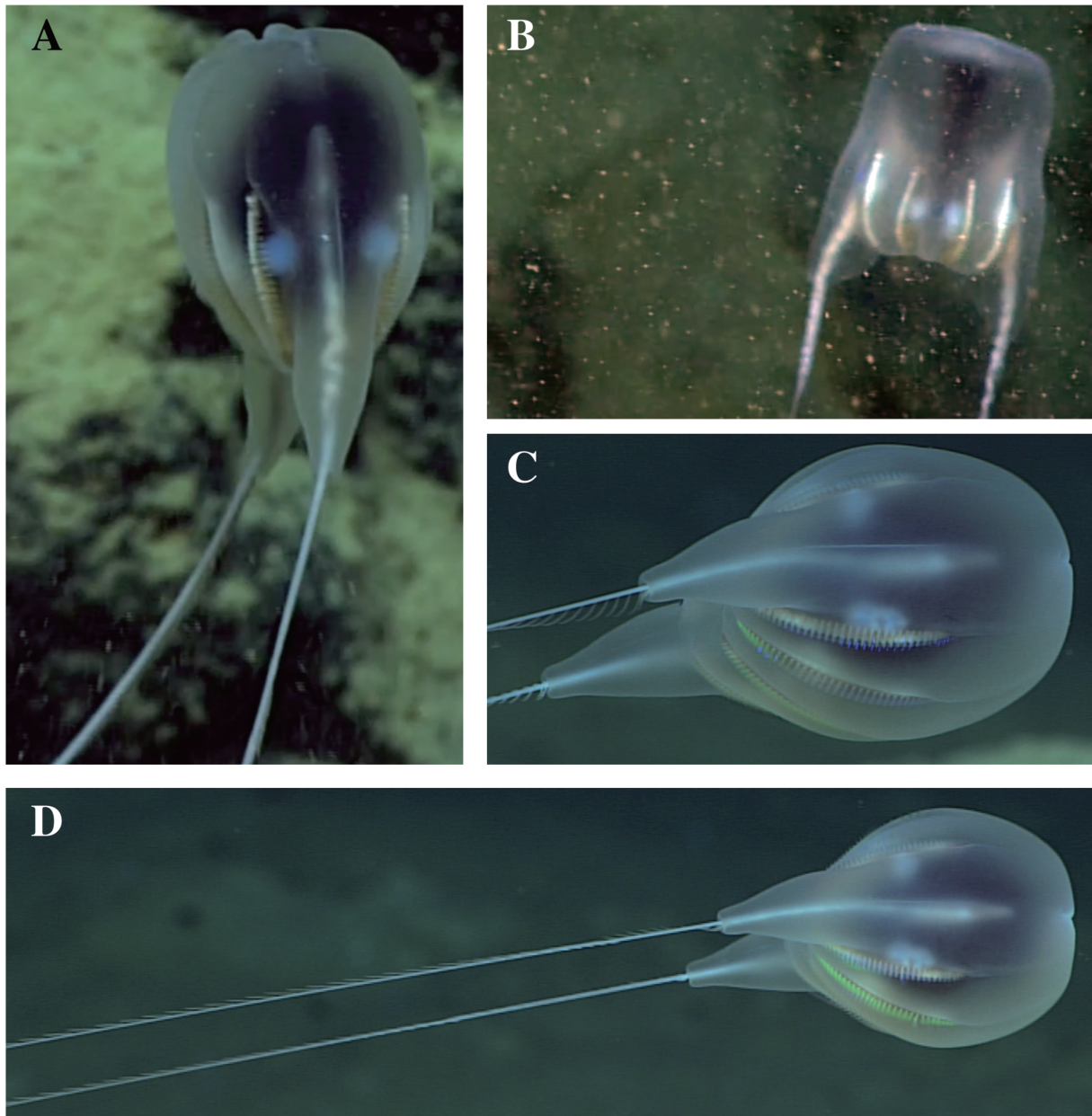


Fig. 1. Stills captured from video observations of *Duobrachium sparksae* n. gen. n. sp. A. First sighting (USNM 1607331), showing body shape in stomodeal plane and tentacles coiling within tentacle sheath inside the arms. 16:30:40 UTC; B. First sighting (USNM 1607331), showing body shape in tentacular plane and gonads beneath all ctenes rows. C and D. Second sighting (USNM 1607332) showing regular tentilla of tentacles and large embryos/eggs within gonads, highlighting the quality of the HD video. 17:37:36 UTC.

Discussion

The discoveries were made 38 km north-northwest of Puerto Rico in the Guajataca Canyon, an erosional canyon approximately 1 km deep that cuts into the 50 km wide Arcicibo Amphitheater (Fig. 4). The Arcicibo Amphitheater is an escarpment topped with a 1.5 km thick sequence of late Oligocene to early Pliocene (28–4 Ma) platform reef carbonates. It is located on the southern margin of the Puerto Rico trench, which descends to a depth of 8.6 km.

Three separate ctenophores of the type described above

were observed at this dive site. The first was observed near a steeply dipping cliff (USNM 1607331). The slope traversed by the ROV during this dive has a staircase topography with approximately 10 km vertical sections of resistant carbonate separated by shallow slopes and ledges of young carbonate ooze and mud. The rocks observed at the discovery sites were often covered in an iron-manganese coating, and a hexactinellid glass sponge appearing to belong to the genus *Atlantisella* was common. The second and third individuals were observed on muddy and gently dipping slopes (USNM 1607332-3). Measurements made

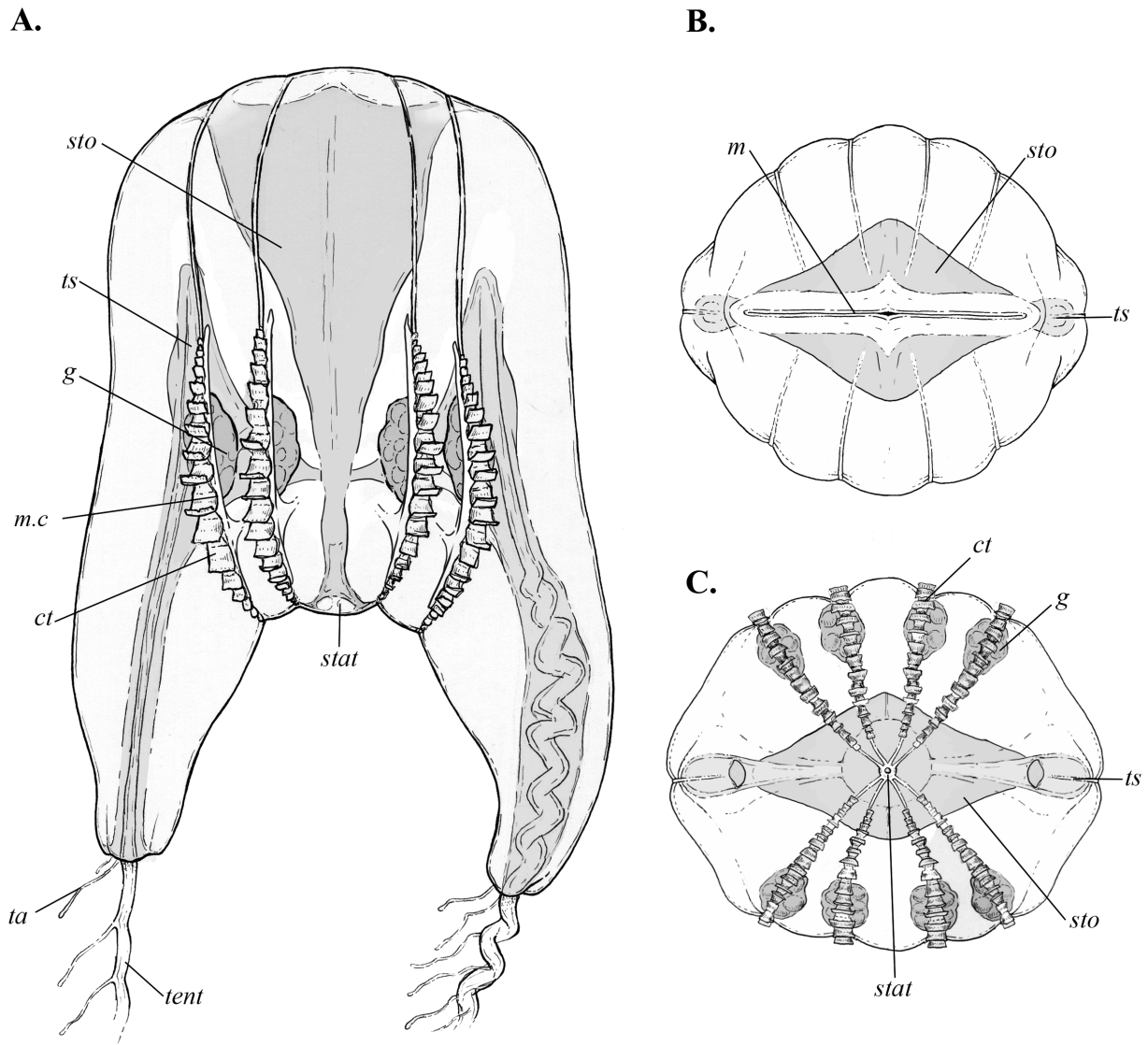


Fig. 2. Line drawing schematic of *Duobrachium sparksae* n. gen. n. sp. A. Tentacular view of the main body of the animal. B. Oral view. C. Aboral view. *ct* - ctene row, *g* - gonads, *m* - mouth, *ta* - tentillum, *tent* - tentacle, *stat* - statocyst, *sto* - stomodaeum. Illustrations by NB.

with the ROV-mounted CTD are presented in Table 1.

The first individual (Animal #1) was observed as the ROV was moving into position at the base of a cliff preparing for benthic observations (USNM 1607331). We suspect most if not all of the tumbling movement of this animal was imparted by ROV thruster wash during the ROV positioning maneuver. However, it appeared that the animal recovered to a vertical orientation after the disruption, and maintained an “oral-up” orientation for the duration of the observation.

Observations of the other two individuals were made as the ROV was transiting horizontally above the slopes—without any observed disruption from the thrusters. One individual (Animal #2; USNM 1607332) was observed holding altitude and position while its tentacles and filaments were apparently tethered to the seafloor. It was unclear how the tentacles were attached to the seafloor

because we were unable to clearly observe the tentacles contacting the sediment, but the tentacles were straight and appeared to be fully extended, as if under tension. With the apparent current moving along the long axis of the animal (oralmost end of the body to the end of the tentacle), the extended tentacles tethered to the seafloor appeared to reach maximum extension and tug at the body, causing the aboral end of the body to react to the tension and tip downward. Two very fine filaments with small particles aggregated to them were observed extending from a point near the mouth and extending, against the current, toward the seafloor in a straight line, again apparently under tension (Fig. 5). We did not observe the point of origin on the body nor the contact point with the seafloor for the filaments, but they were extended in a straight line suggesting a connection near the mouth and contact with the seafloor. Overall, we observed the animal with tentacles extending aborally



Fig. 3. Digital illustration of the habit of *Duobrachium sparksae* n. gen. n. sp. A. tentacular view B. stomodeal view. Illustrations by NB.

behind the body and filaments extending orally—in front of the body. Both were angled toward the seafloor (Fig. 5.) In this configuration, the animal appeared to maintain a constant altitude above the seafloor with the oral end of the body facing into the current. While we do not know the balance of forces, the video sequence suggests this combination of ctene rows, tentacles, and filaments contributed to maintaining a set position above the seafloor.

This behavior is similar to that observed by Lindsay and Miyake (2007) of a benthopelagic ctenophore from the Ryukyu Trench off Japan, although that species was not attached also by its tentacles but rather only by the two filaments. Like Lindsay and Miyake (2007), we found pelagic holothurians to be abundant at this dive site with increasing abundance as the dive progressed (Kennedy et al. 2015). The telepresence-enabled science team observed 22 occurrences of holothurians (*Benthoodytes* sp.) during the dive (MF, unpublished data.) We encountered Animal 3 (USNM 1607333) while it was drifting above the seafloor

with tentacles toward but not touching the seafloor.

Phylogenetic Affinities.—The systematics of Ctenophora are far from settled, with many higher taxa still used for classification known to not be monophyletic (Podar et al. 2001, Simion et al. 2015). For purposes of discussion, we will employ the higher taxonomy provided by the World Register of Marine Species (Mills 2019). Of the orders, only Cydippida and Platyctenida appear to be possible taxonomic homes for the species described herein, with Cestida, Cryptolobiferida, Ganeshida, Lobata, and Thalassocalycida all being unlikely due to major morphological differences. Unfortunately, however, Cydippida is well known as being paraphyletic, being hypothesized to have given rise to all other groups of ctenophores, including Platyctenida (Harbison 1985, Podar et al. 2001, Simion et al. 2015).

The species in question has eight comb rows, retractable tentacles, and a round to squarish body, all typical of species classified as Cydippida, but also likely plesio-

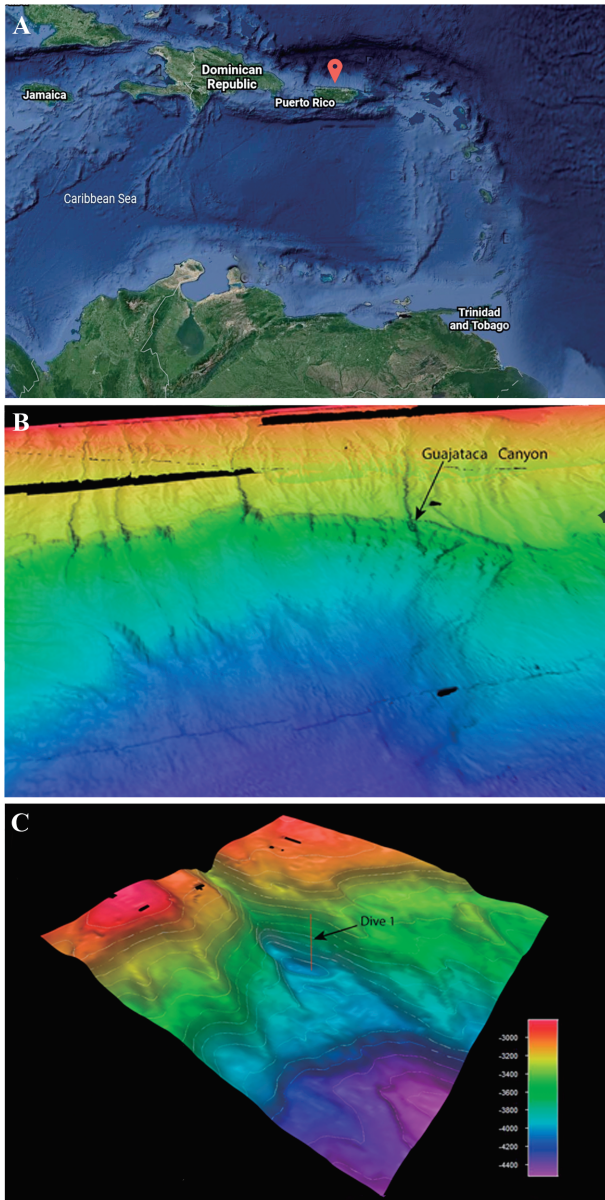


Fig. 4. Location and bathymetry of dive site. A. Dive site north of Puerto Rico, B. Guajataca Canyon and C. The 50 km wide Arcibo Amphitheater on the southern margin of the Puerto Rico trench.

morphies for the phylum (Harbison 1985). Given our observation that *Duobranchium sparksae* n. gen. n. sp. has oral filaments, it is intriguing to compare it to the benthopelagic ctenophore observed by Lindsay and Miyake (2007) anchoring itself to the seafloor by a pair of filaments (presumably oral, but the mouth was not clearly visible). As noted above, that species was not also attached by its tentacles but rather just by the two filaments at the time of observation. This species differs from *Duobranchium sparksae* n. gen. n. sp. in other respects as well, possessing diverticula and lacking tentilla, tentacle arms, and any indication of globular gonads.

The most distinctive character of this new species is the

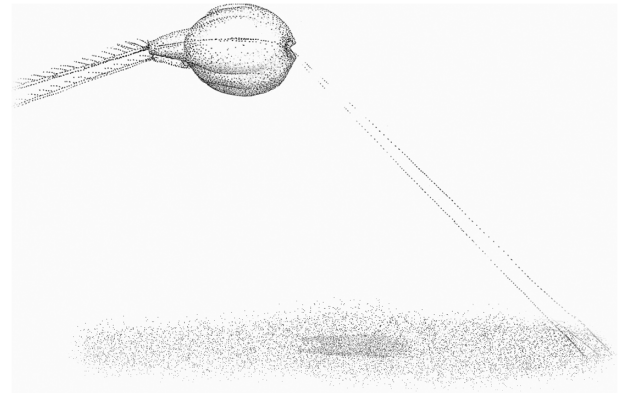


Fig. 5. Artist's interpretation of the configuration of tentacles and filaments of *Duobranchium sparksae* n. gen. n. sp. as observed during the second sighting (USNM 1607332 at 1:14–2:36). The specific insertion point near the mouth and attachment to the seafloor were not observed and are represented here by dashed lines. Illustration by NB.

possession of two prominent tentacle arms or lobes, features that are common in Platyctenida families Ctenoplaniidae Willey, 1896, Savangiidae Harbison & Madin, 1982, Tjalfiellidae Komai, 1922, and particularly Lyroctenidae Komai, 1942. Unlike *Duobranchium sparksae* n. gen. n. sp., platyctenids all possess a skirt or foot used for attachment to substrate, and the majority lack ctene rows as adults (Harbison 1985). Adults of species of Ctenoplaniidae retain comb rows as adults and are capable of limited swimming (Willey 1896). Given that cydippids appear to have given rise to Platyctenida (Podar et al. 2001, Simion et al. 2015), and the combination of traits exhibited by *Duobranchium sparksae* n. gen. n. sp., it seems reasonable to hypothesize that this new ctenophore descends from a lineage that diversified near the origin of Platyctenida.

One additional feature of the present ctenophore suggestive of a relationship with Platyctenida is the large eggs or embryos observed in its gonads. Members of Platyctenida are known to brood their young and have special chambers in which eggs and embryos develop within the meridional canals (Harbison 1985). Irrespective of its phylogenetic significance, the large egg size of *Duobranchium sparksae* n. gen. n. sp., which we estimate to be between 1.5 and 2.0 mm, suggests that the species has non-feeding larvae with limited dispersal capabilities (Thorson 1950), which might in turn limit the geographic range of this species (Emlet 1995). That said, it is not possible to make strong inferences about the meaning of relatively large eggs in this case due to an absence of specimens, which would allow for microscopic investigation of the eggs (or embryos), as well as the lack of a detailed comparative analysis across Ctenophora.

Conclusion

Because of its benthopelagic habit and depth, this

species is unlikely to ever be collected by plankton nets. It could, however, be captured by a suction or detritus sampler, such as that with which the ROV *Deep Discoverer* on the NOAA Ship *Okeanos Explorer* is presently equipped. Eventual collection of specimens of *Duobrachium sparksae* n. gen. n. sp. is highly desirable for a variety of reasons. First, while observations gathered from the existing video makes the species readily recognizable if seen again, and distinguishable from all other known species, it fails to reveal some important internal characters (particularly details of the canal structure). These observations will eventually prove critical for understanding morphological evolution within the phylum. Although a stable and robust phylogenetic framework has yet to emerge for Ctenophora, one can be expected based on the ongoing integration of morphological and molecular data. Future collections of *Duobrachium sparksae* n. gen. n. sp., will also provide access to the wealth of data contained within its genome, which should provide evidence to support a robust phylogenetic placement within Ctenophora, once a reliable phylogenetic framework has been established for the group.

The distinctive species observed during the Océano Profundo Expedition (EX1502) by the NOAA Ship *Okeanos Explorer* has no obvious taxonomic home within any existing genus or species, supporting the hypothesis that the species is new to science. At the time of observation, the NOAA Ship *Okeanos Explorer* and ROV *Deep Discoverer* was not capable of specimen collection and thus the only record of the species is three videos of three different specimens. This presents somewhat of a conundrum because taxonomy relies heavily upon physical type specimens preserved in museums to serve as references to which other material can be compared. Indeed, the idea of using photographic evidence to establish new species has been highly contentious in recent decades (summarized succinctly by Zhang 2017). One difficulty of using photographic evidence in the establishment of new species stems from the fact that taxonomists describing such species must analyze and construe the visual evidence present in photographs and characters may be interpreted incorrectly or unethically, leading to suggestions that the International Code of Zoological Nomenclature (ICZN) be altered to explicitly require the deposition of a preserved type specimen when species are described (Dubois & Nemésio 2007). This draconian rule suggestion has been vigorously resisted by some, with the primary argument being that taxonomists should be the individuals who are best in position to determine the extent to which photographic evidence is sufficient for a given taxonomic problem (Donegan 2008). Nevertheless, the controversy has persisted with many arguing that photographs should never be employed as type specimens (Duboi et al. 2013, Amorim et al. 2016, Ceriaco et al. 2016, Cianferoni & Bartolozzi 2016, Santos et al. 2016), but others recognizing that in certain, infrequent cases that the practice is justified (Marshall & Evenhuis

2015, Pape 2016, Krell & Marshall 2017, Shatalkin & Galinskaya 2017). ICZN has recently taken up the issue in their “Declaration 45” (International Code of Zoological Nomenclature 2017) reiterating that preserved types should be the basis for new species whenever feasible, but stating clearly that the ICZN Code does permit new species to be based upon photographic evidence when “justified by special circumstances, such as when capture or preservation of specimens is not feasible for technical reasons or for conservation concerns, or when specimens must be destroyed to reliably diagnose a new species.”

As noted in our introduction, ctenophores are notoriously difficult to preserve, and contemporary descriptions of new species rely heavily on observations of live animals. Indeed, Lindsay (2017) recently recommended strongly that when new species of ctenophores are described, specimens should be fully documented by photographs and video while alive, and that these materials should be placed in long-term, secure, and well-managed repositories. In the case of *Duobrachium sparksae* n. gen. n. sp., we are establishing the species based on video evidence that has been carefully annotated (Table 1) and placed into a reliable, long-term archive. We have not taken this approach lightly or wish to encourage other species to be described based on photographic evidence alone unless circumstances warrant. In this case, it could be many decades before the opportunity arises to collect this deep-water benthopelagic species. Even if it is collected, it will likely be impossible to preserve its anatomical features (necessitating copious shipboard documentation via photography and videography). Nevertheless, when seen again, *Duobrachium sparksae* n. gen. n. sp. should easily be recognizable based upon the video-based description provided herein. In the meantime, and when that time comes, our formal naming of the genus and species provides unambiguous names serving to facilitate biological communication.

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References

- Amorim DS, Santos CMD, Krell F-T, Dubois A, Nihei SS, Oliveira OMP, Pont A, Song H, Verdade VK, Fachin DA, Kl-
assa B, Lamas CJE, Oliveira SS, Carvalho CJBD, Mello-Patiu
CA, Hajdu E, Couri MS, Silva VC, Capellari RS, Falaschi RL,
Feitosa RM, Prendini L, Pombal JPI, Fernández F, Rocha RM,
Lattke JE, Caramaschi U, Duarte M, Marques AC, Reis RE,
Kurina O, Takiya DM, Tavares M, Fernandes DS, Franco FL,
Cuezzo F, Paulson D, Guénard B, Schlick-Steiner BC, Ar-
thofer W, Steiner FM, Fisher BL, Johnson RA, Delsinne TD,
Donoso DA, Mulieri PR, Patitucci LD, Carpenter JM, Herman
L, Grimaldi D (2016) Timeless standards for species delimita-
tion. *Zootaxa* 4137: 121–128.
- Arafat H, Alamaru A, Gissi C, Huchon D (2018) Extensive mito-
chondrial gene rearrangements in Ctenophora: insights from
benthic Platyctenida. *BMC Evol Biol* 18: 65
- Appletans W, et al. (2012) The magnitude of global marine spe-
cies diversity. *Curr Biol* 22: 2189–2202.
- Cianferoni F, Bartolozzi L (2016) Warning: potential problems
for taxonomy on the horizon? *Zootaxa* 4139: 128–130.
- Ceríaco LMP, Gutiérrez EE, Dubois A (2016) Photography-based
taxonomy is inadequate, unnecessary, and potentially harmful
for biological sciences. *Zootaxa* 4196: 435–445.
- Donegan TM (2008) New species and subspecies descriptions do
not and should not always require a dead type specimen. *Zoo-
taxa* 1761: 37–48.
- Dubois A, Nemésio A (2007) Does nomenclatural availability of
nomina of new species or subspecies require the deposition of
vouchers in collections? *Zootaxa* 1409: 1–22.
- Dubois A, Crochet P-A, Dickinson EC, Nemésio A, Aescht E,
Bauer AM, Blagoderov V, Bour R, de Carvalho MR, Desut-
ter-Grandcolas L, Frétey T, Jäger P, Koyamba V, Lavilla EO,
Löbl I, Louchart A, Malécot V, Schatz H, Ohler A (2013) No-
menclatural and taxonomic problems related to the electronic
publication of new nomina and nomenclatural acts in zoology,
with brief comments on optical discs and on the situation in
botany. *Zootaxa* 3735: 1–94.
- Emler RB (1995) Developmental mode and species geographic
range in regular sea urchins (Echinodermata: Echinoidea).
Evolution 49: 476–489.
- Feuda R, Dorhmann M, Pett W, Philippe H, Rota-Stabelli O,
Lartillot N, Worheide G, Pisani D (2017) Improved modelling
of compositional heterogeneity supports sponges as sister to
all other animals. *Curr Biol* 27, 3864–2870.
- Gershwin LA, Zeidler W, Davie PJF (2010) Ctenophora of Aus-
tralia. In: Davie PJF & Phillips JA (Eds), Proceedings of the
Thirteenth International Marine Biological Workshop, the
Marine Fauna and Flora of Moreton Bay, Queensland. *Mem
Queensl Mus* 54(3): 1–45. Brisbane. ISSN 0079-8835.
- Haddock SHD (2004) A golden age of gelata: past and future
research on planktonic ctenophores and cnidarians. *Hydrobio-
logia* 530/531: 549–556
- Harbison GR (1985) On the classification and evolution of the
Ctenophora. *Origins and Relationships of Lower Inverte-
brates*, pp.78–100.
- Harbison GR, Madin LP, Swanberg NR (1978) On the natural
history and distribution of oceanic ctenophores. *Deep-Sea Res*
25: 233–256.
- International Code of Zoological Nomenclature (2017) Declara-
tion 45—Addition of Recommendations to Article 73 and the
term “specimen, preserved” to the Glossary. *Bull Zool Nomen-
cl* 73: 96–97
- Kennedy BRC, Cantwell K, Sowers D, Quattrini AM, Chea-
dle MJ, McKenna L (2015) EX1502L3 Expedition Report—
Océano Profundo 2015: Exploring Puerto Rico’s Seamounts,
Trenches, and Troughs. Office of Ocean Exploration and Re-
search, Office of Ocean and Atmospheric Research, NOAA,
Silver Spring, MD 20910. OER Expedition Report 2015-02-03,
93 p. doi:10.7289/V5NG4NM8
- Krell F-T, Marshall SA (2017) New Species Described From Pho-
tographs: Yes? No? Sometimes? A Fierce Debate and a New
Declaration of the ICZN. *Insect Syst Divers* 1: 3–19.
- Laumer CE, Fernández R, Lemer S, Combosch D, Kocot KM,
Riesgo A, Andrade SC, Sterrer W, Sørensen MV, Giribet G
(2019) Revisiting metazoan phylogeny with genomic sampling
of all phyla. *Proc R Soc B*, 286: 20190831.
- Lindsay DJ (2017) *Pukia ohtsukai* sp. nov., a new species of “cy-
dippid” ctenophore from Japan. *Plankton Benthos Res* 12(1):
61–65
- Lindsay DJ, Miyake H (2007) A novel benthopelagic ctenophore
from 7,217 m depth in the Ryukyu Trench, Japan, with notes
on the taxonomy of deep-sea cydippids. *Plankton Benthos Res*
2(2): 98–102.
- Marshall SA, Evenhuis NL (2015) New species without dead
bodies: a case for photo-based descriptions, illustrated by a
striking new species of *Marleyimyia* Hesse (Diptera, Bombyli-
idae) from South Africa. *ZooKeys*: 525: 117–127.
- Mills CE (2019) Phylum Ctenophora: list of all valid species
names. Electronic internet document available at: [http://www.
marinespecies.org/aphia.php?p=taxdetails&id=1248](http://www.marinespecies.org/aphia.php?p=taxdetails&id=1248) (Accessed
September, 2019)
- Pape T (2016) Species can be named from photos. *Nature* 537:
307–307.
- Philippe H, Derelle R, Lopez P, Pick K, Borchellini C, Boury-
Esnault N, Vacelet J, Renard E, Houlston E, Quéinnec E,
Da Silva C (2009) Phylogenomics revives traditional views on
deep animal relationships. *Curr Biol* 19(8): 706–712.
- Podar M, Haddock SHD, Sogin ML, Harbison GR (2001) A mo-
lecular phylogenetic framework for the phylum Ctenophora
using 18S rRNA genes. *Molec Phylo Evol* 2(2): 218–230.
- Santos CMD, Amorim DS, Kl-
assa B, Fachin DA, Nihei SS,
De Carvalho CJB, Falaschi RL, Mello-Patiu CA, Couri MS,
Oliveira SS, Silva VC, Ribeiro GC, Capellari RS, Lamas CJE
(2016) On typeless species and the perils of fast taxonomy.

- Syst Entom 41: 511–515.
- Shatalkin AI, Galinskaya TV (2017) A commentary on the practice of using the so-called typeless species. ZooKeys 693: 129–139.
- Simion P, Bekkouche N, Jager M, Quéinnec E, Manuel M (2015) Exploring the potential of small RNA subunit and ITS sequences for resolving phylogenetic relationships within the phylum Ctenophora. Zoology 118: 102–114
- Simion P, Philippe H, Baurain D, Jager M, Richter, DJ, Di Franco A, Roure B, Satoh N, Queinnec, E, Ereskovsky A. (2017) A large and consistent phylogenomic dataset supports sponges as the sister group to all other animals. Curr Biol 27: 958–967.
- Thorson G (1950) Reproduction and larval ecology of marine bottom invertebrates. Biol Rev Camb Philos Soc 25: 1–45.
- Wang M, Cheng F (2019) The complete mitochondrial genome of the Ctenophore *Beroë cucumis*, a mitochondrial genome showing rapid evolutionary rates. Mitochondrial DNA B 4(2): 3774–3775
- Whelan NV, Kocot KM, Moroz TP, Mukherjee K, Williams P, Paulay G, Moroz LL, Halanych KM (2017) Ctenophore relationships and their placement as the sister group to all other animals. Nature Ecol Evol 1(11): 1737.
- Willey A (1897) On *Ctenoplana*. Quart J Micro Sci 39: 323–342.
- World Registry of Marine Species (WoRMS) (2019) Ctenophora. Available at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1248> (Accessed December, 2019)
- Zhang Z-Q (2017) Species names based on photographs: debate closed. Zootaxa 4269: 451–452.
- Zhao Y, Vinther J, Parry LA, Wei F, Green E, Pisani D, Hou X, Edgecombe GD, Cong P (2019) Cambrian sessile, suspension feeding stem-group ctenophores and evolution of the comb jelly body plan. Curr Biol 29: 1112–1125.