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Atolla reynoldsi sp. nov. (Cnidaria, Scyphozoa, Coronatae, Atollidae): A New Species of Coronate Scyphozoan Found in the Eastern North Pacific Ocean ‡

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Simple Summary: This paper describes an unusually large and distinctive deep-sea red medusa with coiled tentacles in the family Atollidae. This family is monogeneric with ten presently accepted species in the genus Atolla. The new medusa is molecularly and morphologically distinct from the five species that we have been able to sample and morphologically distinct from all ten previously described species. We have also observed and collected samples from another two potentially new species. The ocean provides over 98% of the available living space on our planet and we still do not know who is living there or how they interact with one another. This paper adds to the increasing number of new deep-sea species being described as we increase our exploration, and as advances in undersea technology and genetic sequencing become more available.

Abstract: We have observed and collected unusual specimens of what we recognize as undescribed types of the genus Atolla over the past 15 years. Of these, there appear to be three potentially different types. One of these has now been genetically sequenced and compared both morphologically and molecularly with five other Atolla species that have been found in the eastern Pacific. This new variant is so morphologically distinct from other previously described Atolla species that we believe it can be described as a new species, Atolla reynoldsi sp. nov. This species along with two additional types may comprise a new genus. It is also clear that a more accurate and diagnostic morphological key for the genus Atolla needs to be developed. This paper will also provide some potential starting points for a new key to the genus.

Keywords: Atolla; new species; Pacific; coronate; Scyphozoa; ROV; trawl

1. Introduction

The subclass Coronamedusae Calder, 2009 [1] is within the class Scyphozoa Götte, 1887 [2] and contains one order (order Coronatae Vanhöffen, 1892 [3]). There are several families in the Coronatae including the family Atollidae Hickson, 1906 [4] which is monogeneric (Atolla Haeckel, 1880 [5]) with ten potential species [6], some of which are tentative. Atolla specimens have been found in every ocean basin in the world [7], but their contributions to the trophic ecology of pelagic ecosystems have been largely overlooked [8].

The well-documented species of Atolla are A. vanhoeffeni, A. chuni, and A. gigantea. Each of these have morphological characteristics that make them relatively easy to identify and are unique. Many of the other species can be separated into different taxa using the current taxonomic keys [8–11] but this paper shows that some of these morphological characteristics are not useful.

Atolla verrillii and A. valdiviae are both considered to be doubtful species [6] (perhaps both are A. wyvillei). Atolla tenella is described as having very distinctive pigmentation on...
the margin of the exumbrella but other than the illustration in the original description [12], we have not seen an image or mention of this pigmentation despite specific identifications in the literature [13], and Russell [11] considered the validity of the species as uncertain.

*Atolla chuni* was first described from two specimens collected south of the Cape of Good Hope [3] and is distinguished from other *Atolla* species by distinct papillae (‘pearls’) on the lappets. Larson reviewed additional descriptions of *A. chuni*, which he regarded as endemic to the Southern Ocean, and added observations from 1168 specimens [8].

There is still little known about the identity, behavior, or distribution of *Atolla*, one of the most common coronate scyphozoans in the deep ocean. In situ observations from crewned submersibles and remotely operated vehicles have revealed a number of observations on *Atolla’s* swimming and behavior. It is rare that a net tow or a trip to the deep does not reveal one or more *Atolla*. A four-year net study to examine one species (*A. wyvillei*) in the Bay of Biscay [14] found two distinct species (*A. wyvillei* and *A. parva*) with no apparent seasonal or depth differences. Hunt and Lindsay [15] discussed the potential for the hypertrophied tentacle that *Atolla* often exhibits for prey capture (also discussed in an unpublished report by Walker [16]). Direct observations using submersibles revealed that *Atolla* can capture prey including *Nanomia* (a physosnect siphonophore) with this tentacle [17]. Additionally, Moore et al. [18] observed the large red caridean shrimp *Notostomus robustus* feeding on *A. wyvillei*—this feeding continued even after collection.

Thirty years of remotely operated vehicle observations with MBARI have revealed numerous observations of *Atolla* with trailing tentacles—so, when we find jellies that look like *Atolla* but are lacking the long trailing tentacle, it makes us stop and take a longer look. Over the past 15 years using a variety of ROVs, we have collected numerous specimens of three types of *Atolla*-like jellies that lack trailing tentacles. We have also collected other *Atolla* species and have found that existing species keys are often incomplete making it difficult to identify specimens to the species level [8–11]. Despite this, the new species described here is very distinctive and easy to differentiate from all other *Atolla* we have collected.

2. Materials and Methods

Specimens used in this study were collected using a diversity of means. Like many of the earlier scientific studies, some were collected using midwater trawls from the RV *Western Flyer* (Monterey Bay, Southern California, and the Gulf of California) as well as the RV *Kilo Moana* and the RV *Ka’imikai-O-Kanaloa* (In the Hawaiian Islands). The majority of the specimens were collected with the remotely operated vehicles ROV *Tiburon*, ROV *Ventana*, and ROV *Doc Ricketts* using the RV *Point Lobos*, RV *Rachel Carson*, and the RV *Western Flyer* in the Gulf of California, Southern California Bight, and Monterey Bay. Additional materials (*Atolla tenella*) were provided by Kevin Raskoff from the Arctic Ocean [13].

2.1. ROV Collections

We used three remotely operated vehicles (ROV *Ventana*, ROV *Tiburon*, and ROV *Doc Ricketts*) owned and operated by the Monterey Bay Aquarium Research Institute (MBARI) [19]. High-Definition video cameras were mounted on these vehicles and the video signal was conveyed to the surface support vessel specific for each ROV (ROV *Ventana*—R/V *Point Lobos* and R/V *Rachel Carson*; ROV *Tiburon* and ROV *Doc Ricketts*—R/V *Western Flyer*) through the ROV’s tether. At the surface, the video signal was viewed on a high-resolution monitor and was recorded on high-definition tape. More recent observations are with a 4K camera and digital recordings. Comments and descriptions of what is on the recordings are recorded on the audio track of the recording during the dive and can be accessed as needed by MBARI staff or collaborators. Additional environmental data (depth, location, temperature, dissolved oxygen, and salinity) during each dive are collected by instruments on the vehicle and the surface ship and integrated into an accessible and comprehensive relational database (http://dsg.mbari.org/dsg/home accessed on 7 March 2022) that is available to the public.
Specimens for this study were collected in 6.5 L ‘detritus’ samplers, designed for the gentle capture of delicate material in midwater [20], or in a ‘suction’ sampler consisting of a transparent funnel and two meters of flexible tubing leading back to 12 separate 6 L collection cylinders within the ROV tool sled. For the detritus samplers, the ROV pilot positioned the vehicle so that the open cylinder of the sampler enclosed the medusa, then the doors at either end were gently closed by hydraulic rams. For the suction sampler, the funnel, attached to a clear plexiglass tube and flexible tubing, could be extended in front of the ROV [20]. When a medusa was near the wide opening of the funnel, the suction pump was turned on and the animal was gently collected and deposited into a sample container, which was then replaced by an empty container.

Specimens were removed from the collection containers and photographed, if possible, prior to freezing portions or whole animals in liquid nitrogen for later molecular analysis. The remainder of each specimen was then preserved for morphological analysis. One specimen of the new species described in this paper was frozen, dried, and used for CHN elemental analysis as part of a different research project.

### 2.2. DNA Extraction and Amplification

Genomic DNA was isolated from frozen tissue samples using the Monarch Genomic DNA Purification Kit (New England Biolabs, Ipswich, MA, USA) or the DNeasy DNA Blood and Tissue kit (Qiagen, Germantown, MD, USA).

We amplified 18S rDNA gene fragments (1793 bp) with the MitchA and MitchB primers [21]. We had limited success amplifying a few species with universal COI Folmer primers [22]; therefore, we designed new primers based on successful amplifications and on published sequences. Primer sequences were anchored in more conserved areas and analyzed with PrimerQuest program, IDT, Coralville, Iowa, USA (www.idtdna.com/SciTool last accessed 12 December 2018). The COI fragments (697 bp) of the newly-described *Atolla reynoldsi* sp. nov. were amplified using forward primer *Atolla*_white_F2 (CGGGTAGAGGAGGAGAAG) and reverse primer *Atolla*_GB_R2m1(TGAGCTCATACAAACAAAACCAAG), and *Atolla* species B was amplified using forward primer *Atolla*_white_F2 and reverse primer *Atolla*_GB_R3(CATATGATGCGCAYCATACWAYAAAYCCT). All other *Atolla* and corona species were amplified with the primers *Atolla*_GB_F2 (CTGGRCCTTTAATGGGTGATG) and *Atolla*_GB_R2(TGAGCTCATACAACAAARCCT). All fragments were amplified with Phusion High-Fidelity PCR Master Mix with HF buffer (New England BioLabs, Ipswich, MA, USA) in a Veriti PCR thermal cycler (Life Technologies, Carlsbad, CA, USA). PCR conditions were: 98 °C for 30 s; 35 cycles of 98 °C for 30 s, 48 °C for 10 s, and 72 °C for 10 s; and a final extension of 72 °C for 5 min. Gene fragments were sequenced bi-directionally with PCR primers and the BigDyeTerminator v3.1 (Life Technologies, Carlsbad, CA, USA) sequencing kit and analyzed on a 3500xL Genetic Analyzer (Life Technologies, Carlsbad, CA, USA).

### 2.3. DNA Analyses

Bi-directional sequences were assembled and edited sequence fragments with Geneious Prime (v.2022.0.1, https://www.geneious.com last updated 13 January 2022). We aligned data with MUSCLE and estimated the best substitution model with AIC [23] with ModelTest within Geneious Prime. We included all available data from GenBank for closely related species, including *Periphylla periphylla*, *Paraphyllina* sp., *Periphyllopsis* sp., *Nausithoe* sp., *Atorella* sp., species of *Atolla*, and *Linuche* as an outgroup (accession numbers included in the phylogenies). Mitochondrial data were translated with the invertebrate mitochondrial genetic code to detect the presence of stop codons or pseudogenes. We estimated Bayesian phylogenies for 18S rDNA and COI mtDNA separately with MrBayes (v.3.2.7a, [24,25]). Bayesian analyses included multiple runs that ranged from 5–10⁶ generations where we sampled and printed every 1000 generations with six chains after we discarded the first 10% of data. We also estimated likelihood trees with the program IQtree 2 [26,27] with 1000 bootstrap replicates. We trimmed alignments to exclude missing data for likely-
Species ID | Date | Accession Number 18s | Accession Number COI | Sample ID | Depth m | Lat Decimal | Long Decimal | Tentacle Number
---|---|---|---|---|---|---|---|---
*A. gigantea* | 10 August 2015 | OM260068 | OM214504 | D0791D7 | 1112 | 36.531771 | -122.507713 | 24
*A. gigantea* | 14 December 2016 | OM260069 | OM214505 | D0915D5 | 1016 | 36.260438 | -122.593946 | 24
*A. gigantea* | 10 December 2017 | OM260070 | OM214503 | D0995D10 | 897 | 36.748584 | -122.103112 | 24
*A. gigantea* | 19 March 2017 | OM260073 | OM214506 | KOK-T06 | 1584–888 | 19.275 | 156.133333 | 59
*A. gigantea* | 30 May 2021 | OM260072 | OM214502 | D1337x3 | 1253 | 33.850068 | -119.850222 | 24
*A. gigantea* | 30 May 2021 | OM260071 | OM214501 | D1337D5 | 936 | 33.850169 | -119.651754 | 24
*A. parva* | 20 March 2017 | OM260077 | OM214507 | KOK-T7-8 | 838–888 | 19.483333 | 156.133333 | 30
*A. parva* | 21 March 2017 | OM260076 | OM214509 | KOK17-T11 | 1700–1115 | 19.666667 | 156.133333 | 30
*A. parva* | 6 November 2018 | OM260074 | OM214508 | KM-T02.17 | NA | 19.426389 | 156.408611 | 30
*A. parva* | 7 November 2018 | OM260075 | NA | KM18-T05 | NA | 19.426389 | 156.408611 | 30
*A. tenella* | 17 July 2005 | OM260079 | OM214511 | KR–17 | NA | Arctic | NA | NA
*A. tenella* | 25 July 2005 | OM260080 | OM214512 | KR–25 | NA | Arctic | NA | NA
*A. aff. tenella* | 2 March 2015 | NA | OM214513 | D718D7 | 1696 | 24.412664 | -110.095732 | 22
*A. aff. tenella* | 20 March 2017 | OM260060 | OM214515 | KOK17-T09 | 1719–1033 | 19.483333 | 156.133333 | 30
*A. aff. tenella* | 21 March 2017 | OM260061 | OM214516 | KOK17-T11 | 1700–1115 | 19.666667 | 156.133333 | 30
*A. aff. tenella* | 6 November 2018 | OM260058 | OM214517 | KM-T02.18 | NA | 19.426389 | 156.408611 | 30
*A. aff. tenella* | 6 November 2018 | OM260059 | OM214514 | KM-T02.19 | NA | 19.426389 | 156.408611 | 30
*A. tenella* | 7 November 2018 | OM260078 | OM214510 | KM18-T04-13 | 2500 | 19.318333 | 156.133333 | 30
*A. vanhoefeni* | 22 October 2012 | OM260084 | OM214496 | WF-trawl | NA | 36.699558 | -122.049488 | NA
*A. vanhoefeni* | 24 April 2013 | OM260085 | OM214497 | V3709xs2 | 512 | 36.700040 | -122.048422 | NA
*A. vanhoefeni* | 27 May 2015 | OM260081 | OM214498 | V3828D1 | 424 | 36.703304 | -122.052176 | NA
*A. vanhoefeni* | 31 January 2020 | OM260082 | OM214499 | WF-trawl | NA | 36.166666 | -119.25 | NA
*A. vanhoefeni* | 31 January 2020 | OM260083 | OM214500 | WF-trawl | NA | 36.166666 | -119.25 | NA
*A. aff. wyvillei* | 18 March 2010 | OM260067 | OM214523 | V3540x4 | 626 | 36.705400 | -122.053820 | NA
*A. aff. wyvillei* | 22 February 2015 | OM260062 | OM214518 | D710xs11 | 746 | 24.277915 | -110.369673 | 22
*A. aff. wyvillei* | 24 February 2015 | OM260063 | OM214519 | D712xs9 | 706 | 25.430911 | -109.853949 | 22
*A. aff. wyvillei* | 25 February 2015 | OM260064 | OM214520 | D713xs7 | 774 | 25.446143 | -109.848168 | 22
*A. aff. wyvillei* | 9 March 2015 | OM260065 | OM214521 | D723xs9 | 697 | 25.442727 | -109.852022 | 22
*A. aff. wyvillei* | 30 May 2021 | OM260066 | OM214522 | D1337x4 | 985 | 33.850169 | -119.651754 | 24
*A. reynoldsi* sp. nov. | 5 December 2015 | OM260086 | OM214493 | D0830D9 | 1013 | 36.688186 | -122.118768 | 32
*A. reynoldsi* sp. nov. | 6 December 2017 | OM260087 | OM214492 | D0991xs3 | 1878 | 36.548736 | -122.541753 | 32
*A. reynoldsi* sp. nov. | 30 July 2021 | OM260088 | OM214494 | D1349D1 | 3189 | 35.499466 | -123.998767 | 38
*Atolla type B* | 6 December 2017 | OM260056 | OM214495 | D991xs5 | 1783 | 36.548400 | -122.542593 | 60
*Atolla type A* | 30 October 2021 | OM260057 | NA | D1339xs3 | 1253 | 36.700923 | -122.067752 | 59

Temperature, salinity, and oxygen data are available in the appendix Table 1. Sample ID refers to the remotely operated vehicle and the dive number (V for ROV Ventana, T for ROV Tiburon, or D for ROV Doc Ricketts), trawls (T) aboard the RV Kilo Moana (KM), the RV Ka’minik-O-Kanaloo (KOK), or the RV Western Flyer (WF). Two specimens of *Atolla tenella* collected in the Arctic (July 2005) were provided by Kevin Raskoff (KR). NA refers to information that is not available.
Table 2. Physical measurements and water parameters for the collected specimens of Atolla reynoldsi sp. nov.

| Date           | Sample ID | Depth (m) | Temp (°C) | Sal (PSU) | Oxy (mL/L) | Lat (Decimal) | Long (Decimal) | Tentacle Number | Diameter (cm) | Status   |
|----------------|-----------|-----------|-----------|-----------|------------|---------------|----------------|----------------|--------------|-----------|
| 4 April 2006   | T0960s6   | 2848      | 1.657     | 34.621    | 2.29       | 36.573417     | −122.5221505   | 38             | 13          | CHN       |
| 7 April 2006   | T0964s5   | 1400      | 2.897     | 34.5      | 0.81       | 36.328862     | −122.898496    | 26             | NA          | Frozen @  |
| 20 June 2006   | T0994D6   | 1435      | 2.987     | 34.489    | 0.71       | 36.551573     | −122.510275    | 30             | 7.5         | Damaged   |
| 20 October 2009| D0087D8   | 1133      | 3.427     | 34.401    | 0.639      | 36.334888     | −122.917099    | 32             | 8           | Paratype @|
| 9 November 2013| D0546D12  | 2705      | 1.697     | 34.656    | 2.354      | 36.535624     | −122.508432    | 39             | 7.3         | Paratype @|
| 3 August 2014  | D0642D11  | 1500      | 2.777     | 34.541    | 0.858      | 36.533088     | −122.509816    | 36             | 8           | MBARI     |
| 5 December 2015| D0830D9   | 1013      | 3.861     | 34.436    | 0.348      | 36.688186     | −122.118768    | 32             | NA          | Frozen $  |
| 6 December 2017| D0991ss3  | 1878      | 2.229     | 34.402    | 1.373      | 36.546736     | −122.541753    | 32             | 5.8         | MBARI $   |
| 10 August 2018 | D1050D11  | 1445      | 2.906     | 34.528    | 0.821      | 36.534146     | −122.565410    | 26             | 7.7         | Paratype @|
| 30 July 2021   | CASIZ 233651 | 3189  | 1.576    | 34.665    | 2.470      | 35.499466     | −123.99876     | 38             | 8.5         | Holotype $|

All specimens displayed coiled tentacles, no trailing tentacle, a Greek-cross gut morphology, and ridges with spikes on the rhopaliar pedalia. Sample ID refers to the remotely operated vehicle and the dive number (T for ROV Tiburon, or D for ROV Doc Ricketts). NA refers to information that is not available. Diameter is bell diameter from margin to margin including the lappets. The last specimen collected (30 July 2021) is the holotype at California Academy of Sciences (CASIZ 233651); this one was also sequenced ($). There are three paratypes at CASIZ (CASIZ 233650, CASIZ 233652, and CASIZ 233653), two paratypes at MBARI, and two specimens were frozen and sequenced ($). Specimen collected on 4 April 2006 was frozen for CHN elemental analysis as part of a different research project. Specimen collected on 20 June 2006 was damaged in transit to CASIZ and discarded. Short video clips are available (@) online at https://www.mbari.org/supplemental-for-matsumoto-et-al-atolla-reynoldsi-new-species-pub/ (last accessed on 7 March 2022) and in the Supplementary Materials. Video S1: Atolla reynoldsi sp. nov. D0087, 20 October 2009; Video S2: Atolla reynoldsi sp. nov. D0546, 9 November 2013 and Video S3: Atolla reynoldsi sp. nov. D991, 7 April 2006.

Table 3. Physical measurements and water parameters for the collected specimens of Atolla species A.

| Date           | Sample ID  | Depth (m) | Temp (°C) | Sal (PSU) | Oxy (mL/L) | Lat (Decimal) | Long (Decimal) | Tentacle Number | Diameter (cm) | Status   |
|----------------|------------|-----------|-----------|-----------|------------|---------------|----------------|----------------|--------------|-----------|
| 13 June 2002   | T0439      | 1197      | 3.371     | 34.342    | 0.62       | 36.329753     | −122.900502    | 59             | NA          | NA@       |
| 30 October 2021| D1399ss3   | 1253      | 3.264     | 34.515    | 0.764      | 36.700923     | −122.067752    | 59             | 8.5         | &         |
| 14 November 2021| D1402ss9  | 1913      | 2.210     | 34.603    | 1.434      | 36.543934     | −122.536996    | 64             | 5.4         | &@        |

These specimens displayed straight tentacles, no trailing tentacle, an evaginated Greek-cross gut morphology (see Section 3.2.3), and no papillae or spike ridges on the rhopaliar pedalia. The overall shape is tall with a distinctive large rounded dome. Sample ID refers to the remotely operated vehicle and the dive number (T for ROV Tiburon, or D for ROV Doc Ricketts). Diameter is bell diameter from margin to margin excluding the lappets. Samples collected in 2021 are at MBARI (€), the specimen observed in 2002 was not collected. Short video clips are available (@) in the Supplementary Materials section and online at https://www.mbari.org/supplemental-for-matsumoto-et-al-atolla-reynoldsi-new-species-pub/ (last accessed on 7 March 2022) Video S4: Atolla gigantea D0315, November 5 2011; Video S5: Atolla reynoldsi species A D1399, 30 October 2021 and Video S6: Atolla reynoldsi species A D1402 14 November 2021. NA refers to information that is not available.

Table 4. Physical measurements and water parameters for the collected specimens of Atolla species B.

| Date           | Sample ID  | Depth (m) | Temp (°C) | Sal (PSU) | Oxy (mL/L) | Lat (Decimal) | Long (Decimal) | Tentacle Number | Diameter (cm) | Status   |
|----------------|------------|-----------|-----------|-----------|------------|---------------|----------------|----------------|--------------|-----------|
| 18 November 2004| T764       | 3247      | 1.603     | 34.6      | 2.61       | 36.329555     | −122.899157    | 39             | 5.5         | &         |
| 22 June 2006   | T0998D4    | 3275      | 1.632     | 34.589    | 2.41       | 36.341234     | −122.916458    | 32             | 1.7         | &         |
| 14 April 2007  | T1088D4    | 2570      | 1.807     | 34.437    | 2.12       | 36.551916     | −122.502087    | 32             | NA          | NA        |
| 20 May 2014    | D0613ss8   | 3302      | 1.697     | 34.652    | 2.47       | 36.501258     | −122.866931    | 42             | 7.4         | &         |
| 6 December 2017| D0991ss5   | 1783      | 2.363     | 34.592    | 1.271      | 36.548000     | −122.542593    | 60             | NA          | $@        |

All specimens displayed coiled tentacles, no trailing tentacle, a Greek-cross gut morphology, and papillae but no spiked ridges. D0991ss5 was frozen and used for DNA sequencing ($) while the specimens from 2004, 2006, and 2014 are at MBARI (€). The specimen collected in 2007 was photographed in the lab but not examined further. Short video clips are available (@) in the Supplementary Materials section and online at https://www.mbari.org/supplemental-for-matsumoto-et-al-atolla-reynoldsi-new-species-pub/ (last accessed on 7 March 2022) Video S7: Atolla species B D991 December 6 2017 and Video S8: Atolla species B D613 20 May 2014. NA refers to information that is not available.
Figure 1. Images of *Atolla reynoldsi* sp. nov. from T960 on 4 April 2006. (a) Laboratory photo of *Atolla reynoldsi* sp. nov. (photo by Rob Sherlock). Diameter from margin to margin (excluding lappets) is 8.5 cm and tentacles were coiled in situ. (b) In situ image of *Atolla reynoldsi* sp. nov. The spikes and spike ridges on the lappets and the coiled tentacles are visible.

Figure 2. (a) Laboratory photo of *Atolla* species A taken in the lab (photo by SHDH) of the specimen collected on 30 October 2021 (D1399). Diameter from margin to margin (excluding lappets) is 8.5 cm. (b) In situ image of *Atolla* species A (D1402) photographed on 14 November 2021 at a depth of 1913 m, 5.4 cm in diameter.

Figure 3. (a) Laboratory photo of *Atolla* species B (photo by Rob Sherlock) of the specimen collected on 14 April 2007 (T1088). (b) In situ image of *Atolla* species B (T1088) photographed on 14 April 2007 at a depth of 2570 m.
3.1.2. *Atolla reynoldsi* sp. nov.

Table 2 and Figure 1 refer to *Atolla reynoldsi* sp. nov. *Atolla reynoldsi* sp. nov. has 26–39 tentacles that are coiled in situ, a Greek-cross gut morphology with smooth edges, spiked ridges and papillae on the rhopaliar pedalia and no trailing tentacle.

3.1.3. *Atolla* Species A

Table 3 and Figure 2 refer to *Atolla* species A. *Atolla* sp. A has 59–64 tentacles, a Greek-cross gut morphology with both invaginations and evaginations, no spiked ridges or papillae on the rhopaliar pedalia, and no trailing tentacle.

3.1.4. *Atolla* Species B

Table 4 and Figure 3 refer to *Atolla* species B. *Atolla* sp. B has 32–60 tentacles, a Greek-cross gut morphology with smooth edges, no spiked ridges, but may have some papillae on the rhopaliar pedalia, and no trailing tentacle.

3.2. Morphological Distinctions

3.2.1. Pigmentation

Currently, only two of the described *Atolla* species have pigment spots as one of their diagnostic characters, whereas the new species has none. *Atolla vanhoeffeni* has eight very distinct pigment spots that were first identified by Vanhoffen [28] and used by Russell [29] to erect the new species *A. vanhöffeni*. These pigmentation spots are on the subumbrellar walls of the stomach where the gastric cavity begins to narrow (Figure 4a); they are not pores. Hartlaub [12] described another new species (*A. tenella*) that has two pigment spots on the margin and centered on the rhopaliar pedalia (Figure 4b). While the pigmentation for *A. vanhoeffeni* can be easily found on specimens, we have not observed or seen any photographs of the pigmentation for *A. tenella*. The specimens used for the original species description were small (5–10 mm), and since our specimens came from the same expedition as Raskoff et al. [13] and these were identified as *A. tenella*, we have kept that identification (note, a preserved sample from that expedition did not have pigment spots) and have tentatively identified many of our Hawaiian samples as *A. aff. tenella*? based on a close molecular similarity with the Arctic Ocean *A. tenella* (Appendix A Table A3).

![Figure 4](image-url)

*Figure 4.* Line drawing showing pigmentation location and patterns for pigmentation observed on the (a) oral side of *Atolla vanhoeffeni* (modified from Russell 1957 [28]) and the (b) aboral side of *A. tenella* (modified from Hartlaub 1909 [12]). cm coronal muscle; go gonad; l lappet; rh rhopalium; te tentacle; rs radial septa; ps pigment spot; rp rhopaliar pedalia.
3.2.2. Papillae

*Atolla chuni* is the only described species of *Atolla* with protrusions labeled as warts on the exumbrellar surface [8]. *A. chuni* also has paired warts (sw) on top of the radial septa (Figure 5a) and another 7–9 warts (with one in the center and the others in two lateral rows) on the rhopaliar pedalia (Figure 5a). We are using the term papillae rather than warts for *A. reynoldsii* sp. nov. for the solitary protrusions as papillae is more commonly used in the literature for cnidarians. We are also using the term spikes to reflect the protrusions on ridges (for *Atolla reynoldsi* sp. nov.) as they have a variety of morphologies (Figure 5b–d) and are not simple rounded warts as in *A. chuni*. We have not included *A. chuni* in our analysis as we have never found a specimen that meets this description. *Atolla reynoldsi* sp. nov. has distinct ridges (~7) on each side of the rhopaliar pedalia that have spikes that are rounded close to the margin but pointed closer to the end of the pedalia. There are four solitary papillae closest to the body disc and no papillae over the radial septa. *Atolla* sp. A lacks papillae or spikes on ridges while *Atolla* sp. B has papillae (small and lined up in two rows like those of *A. chuni*) on the rhopalia but not over the septa. There are no spiked ridges in *Atolla* sp. B.

Figure 5. (a) Line drawing showing the pedaliar wart (pw) and septal wart (sw) pattern for *Atolla chuni* (from Larson [3] and used with permission under license number 5203151138336) and (b) the spikes on the rhopaliar pedalia for *Atolla reynoldsii* sp. nov. (drawn from photographs). Dissection microscope images (c) 7.5 × and (d) 30 × of the papillae (pp), spikes (sp), and the spike ridges (spr) of *Atolla reynoldsii* sp. nov (D1369D1). There were no septal warts observed. l lappet; rp rhopaliar pedalia; rh rhopalium; cm coronal muscle; te tentacle; go gonad; rs radial septa; pw pedaliar wart; sw septal wart; pp papillae; sp spike; spr spiked ridge.
3.2.3. Stomach Morphology

There have been two basic stomach patterns (Figures 4b and 6a) described for species within the genus *Atolla* [28]. *Atolla vanhoeffeni* presents a simple cross-shaped pattern (Figure 6a) while the basal stomach pattern for the other *Atolla* species is more similar to a four-leaf clover (Figure 6b). All three new *Atolla* types observed in Monterey are not only larger than the other described species (with the exception of *Atolla gigantea*), but also exhibit a different stomach pattern. We have termed this new morphology a Greek-cross shape (similar to Maltese cross shape with oval arms) and it presents as a thin base that then expands into a vase shape and ends with a shallow indentation near the edge of *Atolla reynoldsi* sp. nov. (Figure 6c) and *Atolla* sp. B, or a much more globular shape with very deep indentations near the margin edge for *Atolla* sp. A. (Figure 6d). Both *Atolla reynoldsi* sp. nov. and *Atolla* species B have this Greek-cross stomach pattern with smooth edges (Figure 6c) while *Atolla* species A has the Greek-cross stomach pattern with evaginations along the stomach and invaginations close to the center of the medusa and evaginations at the margin near the coronal muscle (Figure 6d).

![Figure 6](image_url)

**Figure 6.** Line drawings showing the stomach patterns for (a) *Atolla vanhoeffeni*, (b) *Atolla wyvillei*, (c) *Atolla reynoldsi* sp. nov.—(D1369) in situ, 8.5 cm in diameter showing four narrow bases at the center of the medusa that expand into a vase-like shape before ending with a shallow indentation. (d) *Atolla* sp. A (D1399) in lab, 8.5 cm in diameter showing a much more rounded expansion with a much deeper indentation and the edges of the rounded expansion show invaginations near the center of the stomach and evaginations around the margin near the coronal muscle (cm). go gonad; l lappet; rh rhopalium; te tentacle; rs radial septa; ps pigment spot; rp rhopaliar pedalia.
3.2.4. Radial Septa

Radial septa are easily observed both in situ and in preserved specimens and have been used as a diagnostic character in keys for the genus *Atolla*. Our observations have revealed that preservation has an impact on the morphology of the septa. Specifically, for *A. gigantea*, the septa are clearly divergent when examining in situ frame grabs (Figure 7a) but appear to be straight when looking at preserved specimens (Figure 7b). This could be simply due to contraction of the bell, but it still makes the use of this morphology suspect for taxonomy as the amount of contraction would likely vary with fixative type and concentration.

![Figure 7. (a) In situ image of *Atolla gigantea* (D915) showing what appears to be divergent septa and (b) a photograph of the same specimen preserved in 5% formalin showing what appear to be straight septa. This specimen was 7.6 cm in diameter.](image)

3.2.5. Tentacles

The appearance of a hypertrophied tentacle is generally used as a diagnostic character for the genus *Atolla*. The number of tentacles has been used as another diagnostic but there appears to be a great deal of variability in the number for each species. At this point, there does not seem to be enough confidence to use tentacle number as a diagnostic nor (if these three new species are to be kept in the genus *Atolla*) can the hypertrophied tentacle be used. Nine of the ten specimens of *Atolla reynoldsi* sp. nov. observed had coiled tentacles; the tenth was able to coil some of the tentacles but then released the coil to display tentacles more similar to other *Atolla* species.

3.3. Molecular Results

We sequenced three individuals of *A. reynoldsi* sp. nov. for the COI mtDNA and 18S rDNA fragments in addition to 30 new sequences of close relatives for statistical analyses. (Table 1, GenBank accession #’s OM214492-OM214523 and OM260056-ON260088). We sequenced nine other coronate species for 18s rDNA and one for COI mtDNA (Table 5, GenBank accession numbers OM201135-OM201143 and OM237455).

Sequencing efforts for *Atolla* sp. A are ongoing: we have gotten some preliminary 18S rDNA sequences but they are not included in Figure 8 as they are only ~300 bp long and identical to the sequence obtained for *Atolla* sp. B. The alignments of 18S rDNA were conserved among *Atolla, Periphylla, Periphylopsis, Linuche*, and *Nausithoe* species and resulted in very few mutations. As a result, phylogenies were mostly unresolved, especially within genera. However, *Atolla reynoldsi* sp. nov. was distinct from all other *Atolla* species (Figure 8).
Table 5. Cororate genera sequenced for rooting in the 18S rDNA molecular tree.

| Species ID          | Date       | Accession Number     | Sample ID | Depth m | Lat Decimal | Long Decimal |
|---------------------|------------|----------------------|-----------|---------|-------------|--------------|
| Periphylla periphylla | 15 November 2015 | OM201140 D1218 ss6 392 36.698180 |
| Paraphyllina sp.    | 27 May 2019 | OM201136 D1218 ss1 1761 28.182585 |
| Paraphyllina sp.    | 9 March 2015 | OM201139 D0780 D11 534 36.150820 |
| Paraphyllina sp.    | 18 November 2019 | OM201138 D1218 ss12 384 36.695557 |
| Paraphyllina sp.    | 1 July 2015 | OM201139 D0780 D11 534 36.150820 |
| Paraphyllina sp.    | 15 November 2015 | OM201140 D1218 ss6 392 36.698180 |
| Periphylla periphylla | 15 November 2015 | OM201141 D1218 ss12 384 36.695557 |
| Periphylla periphylla | 16 November 2015 | OM201142 D1219 D10 923 36.544387 |

Temperature, salinity, and oxygen data are available in the appendix. Sample ID refers to the remotely operated vehicle and the dive number (D for ROV Doc Ricketts) followed by the type of collection (ss for Suction Sample and D for Detritus Sample).

Figure 8. Bayesian and Likelihood estimates of phylogenetic trees for cororate jellies with an 1826 base pairs (bp) alignment of the 18S rDNA fragment with a GTR + I + Γ selection model and an 892 bp alignment of the COI mtDNA fragment with a GTR + I + Γ selection model. Posterior probabilities and bootstrap results displayed as triangles (see legend). Support of nodes with below threshold value not shown.
The COI mtDNA alignments were more informative and provided delineation among and even within species from distinct localities with full Bayesian and likelihood support (Figure 8). *Atolla reynoldsi* sp. nov. differed from its closest relative, another undescribed type of *Atolla* sp. ‘B’ by about ~22% for the GTR + I + Γ selection model. This differentiation was far greater than among many other described species of *Atolla* (Figure 8). We do not yet have COI mtDNA for *Atolla* sp. A.

4. Discussion

4.1. Systematics

Class Scyphozoa Götte, 1887 [1]
Subclass Coronamedusae Calder, 2009 [2]
Order Coronatae Vanhöffen, 1892 [3]
Family Atollidae Hickson, 1906 [4]
Genus *Atolla* Haeckel, 1880 [5]
*Atolla reynoldsi* sp. nov.
Figures 1, 5b–d and 6c.

Diagnosis: *Atolla reynoldsi* sp. nov. can have from 26–39 tentacles and rhopalia. The overall shape is flattened although the center zone is a rounded dome, albeit not very tall (Figure 1). The tentacles in situ are usually coiled and a hypertrophied tentacle has not been observed. There are ~nine lateral ridges along the pedalia that have some spikes of various heights (Figure 5b–d). The gut has a distinctive Greek-cross morphology (Figure 6c). Diagnostic characters separating this new species from extant *Atolla* species include the spiked ridges and papillae on the exumbrellar surface of the rhopaliar pedalia, the ability to coil the tentacles, the Greek-cross gut morphology, and the lack of a hypertrophied tentacle. The gonads are oval when immature but become large and horseshoe-shaped when mature. The radial septa are straight or slightly divergent and extend beyond the coronal muscle.

Type material: The type specimen was collected on 30 June 2021 at 3189 m depth, at 35°29’58.0776” N and 123°59’55.536” W in Monterey Bay, California. The holotype specimen and three paratype specimens have been deposited at the California Academy of Sciences (Holotype: CASIZ no. 233651; Paratypes: CASIZ 233650, CASIZ 233652, and CASIZ 233653). Two additional paratypes are housed at the Monterey Bay Aquarium Research Institute (MBARI). A total of ten specimens have been collected between April 2006 and June 2021 (Table 1) in Monterey Bay (eastern North Pacific Ocean) at depths between 1013 and 3189 m.

Etymology: Named after the first volunteer at the Monterey Bay Aquarium (Jeff Reynolds) who guarded a beached whale on Del Monte Beach overnight so that the Aquarium could retrieve it and prepare it for eventual overhead display.

Systematic remarks: The order Coronatae is identified by the separation of the exumbrella into two concentric zones by a circular coronal groove. The central zone is a circular disc or dome while the marginal zone is divided by radiating grooves into thickened pedalia, with peripheral lappets. The presence of more than eight rhopalia place it into the family Atollidae, which is currently monogeneric.

The previously described number of rhopalia in the genus *Atolla* is 16–32. However, *Atolla reynoldsi* sp. nov. has up to 39 rhopalia and the *Atolla* sp. A and *Atolla* sp. B have up to 64 rhopalia. While it is possible that these types with 32 or more rhopalia might be a new genus, we are not comfortable at this time in making this recommendation as we have not examined all 10 putative species or completed the molecular analysis for *Atolla* sp. A and *Atolla* sp. B. Therefore, we recommend that the new diagnosis for the family Atollidae be modified to include up to 64 tentacles and rhopalia. We are in the process of writing up new species descriptions for *Atolla* sp. A and *Atolla* sp. B as soon as we complete our molecular analysis of these two types.
4.2. Molecular Analysis

The 18S rDNA fragment was highly conserved and resulting phylogenies were paraphyletic among Atolla, Periphylla periphylla, Paraphyllina, and Periphyllopsis species. Despite unresolved polytomies, the 18S fragment clearly delineated between Atolla reynoldsi sp. nov. and Atolla sp. B, while other species of Atolla had identical residues.

The COI mtDNA locus provided better resolution and stronger support for the delineation of species and for the inclusion of A. reynoldsi sp. nov. into the Atolla genus. Atolla reynoldsi sp. nov. differed from its closest relatives, two undescribed species of Atolla (sp. A and B) by about ~22% for the GTR + I + I selection model. This differentiation was far greater than many other described species of Atolla but they were still closer to Atolla than other genera in the order (Figure 8). Atolla reynoldsi sp. nov. and Atolla spps. A and B were more distantly related to other Atolla species, although there was full likelihood and Bayesian support for their inclusion into the Atolla genus.

The remainder of Atolla species were more closely related and their interrelationships were less clearly resolved. Atolla tenella from the Arctic region (as identified by Raskoff et al. [13] and what we identified as A. aff. tenella from Hawaii (based on having 30 tentacles) were distinct from each other, and neither had the pigment spots that were indicative of the species in the original description [12]. Published COI sequences for A. wyvillei from the North Atlantic also differed from the COI fragment of A. aff. wyvillei from the Gulf of California and Southern California. Atolla gigantea, A. vanhoeffeni, and A. parva were more easily identified morphologically and sequence data were congruent with morphology.

5. Conclusions

Our investigations reveal that there are types of Atolla-like coronates that do not fall within the current taxonomic descriptions of the family Atollidae or the genus Atolla. Until more information can be gathered, we are proposing that Atolla reynoldsi sp. nov. remain within Atolla (along with the other two potential new types A and B) but that more work needs to be completed to clarify their placement within the coronates. We do plan on continuing this work and describing these two new types.

Despite the lack of an adequate key, it is clear that that Atolla reynoldsi sp. nov. is molecularly distinct from the Atolla species that we have been able to collect and that it is morphologically distinct from all ten described Atolla species (although sharing the presence of papillae with A. chuni).

The two additional types (Atolla species A and Atolla species B) may likewise be new species but we do not have enough samples at this time to make that claim. All three types (Atolla reynoldsi sp. nov., Atolla species A, and Atolla species B) may need to be placed into a new genus due to their distinct stomach morphology and the lack of a trailing tentacle, but until further work is completed, we recommend that they remain within the genus Atolla and that the family description (Atollidae) be modified to include 16–62 rhopalia rather than 16–32 rhopalia.

Current keys for Atolla species need to be revised as there are no keys that include all ten species, the number of tentacles is more variable than original authors had noted, and the use of radial septa in the keys is problematic, as determining if they are divergent or straight is somewhat subjective and can be changed by preservation. We recommend that additional examination of all ten described species be completed, ideally with specimens from the type localities, and that a more accurate key be developed for the described species. A table listing diagnostic traits for species included in this analysis is provided as an appendix (Table 2).

Erection of a better dichotomous key for the genus will require better identification of the putative existing species so we suggest that specimens from the original locations be obtained and photographed/sequenced in order to create a more accurate key. It is possible that some of the described species are not valid species and will need to be placed into an existing species. Atolla vanhoeffeni can be clearly distinguished morphologically from all
other extant species (based on the pigment spots) and it also groups as a separate species molecularly. While *A. tenella* may also have pigmentation spots, we have been unable to find any photographic evidence and the validity of this species should be examined as it might just be *A. wyvillei* [11]. The use of radial septa orientation (divergent or straight) is problematic as fixation causes this to change. *Atolla wyvillei* is supposed to have septa that pass the coronal muscle but we have found that other specimens that classify as *A. reynoldsi* sp. nov., *A. parva*, and *A. gigantea* also have septa that extend beyond the coronal muscle. *Atolla chuni* is known to have papillae or warts and these have been well documented by Larson and are quite different from those of *A. reynoldsi* sp. nov., but we were not able to find *A. chuni* specimens to sequence.

**Supplementary Materials:** The following videos are available online at https://www.mdpi.com/article/10.3390/ani12060742/s1, Video S1: *Atolla reynoldsi* sp. nov. D0087, 20 October 2009. Video S2: *Atolla reynoldsi* sp. nov. D0546, 9 November 2013. Video S3: *Atolla reynoldsi* sp. nov. T964, 7 April 2006. Video S4: *Atolla gigantea* D0315, 11/5/2011. Video S5: *Atolla* species A D1399, 30 October 2021. Video S6: *Atolla* species A D1402 14 November 2021. Video S7: *Atolla* species B D991 6 December 2017. Video S8: *Atolla* species B D613 20 May 2014.

**Author Contributions:** G.I.M. provided the initial impetus for this manuscript with substantial input from B.H.R. and S.H.D.H. L.M.C. provided the molecular sequencing of the specimens and L.M.C., S.B.J. and S.H.D.H. provided analysis of the resulting molecular trees. S.B.J. created Figure 8 and Appendix A Table A3; S.H.D.H. created Appendix A Table A2. All five authors contributed to the final manuscript creation, review, and editing. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** The work did not require Institutional Review Board approval as the study focused on the description of a new invertebrate species and used other related species that are not identified as endangered or threatened. No vertebrates or cephalopods were involved, so those relevant animal care procedures were not invoked.

**Data Availability Statement:** COI and 18S sequence fragments have been deposited in GenBank (2022) with accession numbers OM260056-OM260088, OM214492-OM214523, OM201135-OM201143, OM237455, and OM202513.

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**Conflicts of Interest:** The authors declare no conflict of interest.
Appendix A

Table A1. Water parameters and collection information for sequenced *Atolla* and other coronate specimens. Sample ID refers to the remotely operated vehicle and the dive number (V for ROV *Ventana*, T for ROV *Tiburon*, or D for ROV *Doc Ricketts*), blue-water SCUBA dive (BW) or trawls (T) aboard the RV *Kilo Moana* (KM), the RV *Ka'imikai-O-Kanaloa* (KOK), or the RV *Western Flyer* (WF). Two specimens of *Atolla tenella* collected in the Arctic were provided by Kevin Raskoff (KR). Some information was not available (NA).

| Species ID | Date               | Sample ID | Depth m | Temp °C | Sal PSU | Oxy ml/L | Lat Decimal | Long Decimal |
|------------|--------------------|-----------|---------|---------|---------|----------|-------------|--------------|
| *A. gigantea* | 10 August 2015     | D0791D5   | 1112    | 3.809   | 34.457  | 0.373    | 36.531771   | −122.507713  |
| *A. gigantea* | 14 December 2016   | D0915D5   | 1016    | 3.852   | 34.467  | 0.411    | 36.260438   | −122.593946  |
| *A. gigantea* | 10 December 2017   | D0995D10  | 897     | 4.199   | 34.427  | 0.297    | 36.748584   | −122.103112  |
| *A. gigantea* | 19 March 2017      | KOK-T06   | NA      | NA      | NA      | NA       | 19.275      | 156.13333    |
| *A. gigantea* | 30 May 2021        | D1337D5   | 936     | 4.436   | 34.45   | 0.321    | 33.850169   | −119.651757 |
| *A. parva*    | 20 March 2017      | KOK-T7/8  | NA      | NA      | NA      | NA       | 19.483333   | 156.13333    |
| *A. parva*    | 21 March 2017      | KOK17-T11 | NA      | NA      | NA      | NA       | 19.666667   | 156.13333    |
| *A. parva*    | 6 November 2018    | KM-T02.17 | NA      | NA      | NA      | NA       | 19.426389   | 156.408611  |
| *A. parva*    | 7 November 2018    | KM18 T05  | NA      | NA      | NA      | Arctic   | 19.318333   | 156.185833  |
| *A. tenella*  | 17 July 2005       | KR-17     | NA      | NA      | NA      | NA       | Arctic      |              |
| *A. tenella*  | 25 July 2005       | KR-25     | NA      | NA      | NA      | NA       | Arctic      |              |
| *A. aff. tenella* | 2 March 2015   | D718D7    | 1696    | 2.633   | 34.615  | 1.212    | 24.412664   | −109.095732 |
| *A. aff. tenella* | 20 March 2017  | KOK17-T09 | NA      | NA      | NA      | NA       | 19.483333   | 156.13333    |
| *A. aff. tenella* | 21 March 2017  | KOK17-T11 | NA      | NA      | NA      | NA       | 19.666667   | 156.13333    |
| *A. aff. tenella* | 6 November 2018 | KM- T02.18 | NA      | NA      | NA      | NA       | 19.426389   | 156.408611  |
| *A. aff. tenella* | 6 November 2018 | KM-T02.19 | NA      | NA      | NA      | NA       | 19.426389   | 156.408611  |
| *A. tenella*  | 7 November 2018    | KM18 T04-13 | 2500    | 34.251  | 0.343   | 36.700040  | −122.049488 |
| *A. vanhoeffeni* | 22 October 2012  | WF trawl  | NA      | NA      | NA      | NA       | 36.699558   | −122.049488 |
| *A. vanhoeffeni* | 24 April 2013   | V3709ss2  | 512     | 6.002   | 34.251  | 0.343    | 36.700040   | −122.049488 |
| *A. vanhoeffeni* | 27 May 2015      | V3828D1   | 424     | 6.876   | 34.179  | 0.924    | 36.703950   | −122.052176 |
| *A. vanhoeffeni* | 31 January 2020  | WF-D1243trawl | NA      | NA      | NA      | NA       | 36.166666   | −119.25     |
| *A. aff. wyvillei* | 18 March 2010  | V3540ss4  | 626     | 5.077   | 34.319  | 0.195    | 36.705400   | −122.053820 |
| *A. aff. wyvillei* | 22 February 2015 | D710ss11  | 746     | 6.020   | 34.509  | 0.023    | 24.277515   | −109.360873 |
| *A. aff. wyvillei* | 24 February 2015 | D712ss9   | 706     | 5.997   | 34.516  | 0.032    | 25.430911   | −109.853949 |
| *A. aff. wyvillei* | 25 February 2015 | D713ss7   | 774     | 6.002   | 34.516  | 0.032    | 25.446143   | −109.848168 |
| *A. aff. wyvillei* | 9 March 2015     | D723ss9   | 697     | 5.956   | 34.516  | 0.034    | 25.442727   | −109.852024 |
| *A. aff. wyvillei* | 30 May 2021      | D1337ss4  | 985     | 4.436   | 34.45   | 0.321    | 33.850169   | −119.651757 |
Table A1. Cont.

| Species ID          | Date               | Sample ID | Depth m | Temp °C | Sal PSU | Oxy ml/L | Lat Decimal | Long Decimal |
|---------------------|--------------------|-----------|---------|---------|---------|----------|-------------|--------------|
| A reynoldsi sp. nov.| 5 December 2015    | D0830D9   | 1013    | 3.861   | 34.436  | 0.348    | 36.688186   | -122.118768  |
| A reynoldsi sp. nov.| 6 December 2017    | D0991ss3  | 1878    | 2.229   | 34.602  | 1.373    | 36.548736   | -122.541753  |
| A reynoldsi sp. nov.| 30 July 2021       | D1369D1   | 3189    | 1.576   | 34.665  | 2.470    | 35.499466   | -123.99876   |
| Atolla type A       | 30 October 2021    | D1399-ss3 | 1253    | 3.264   | 34.515  | 0.764    | 36.7009226  | -122.067752  |
| Atolla type B       | 6 December 2017    | D991ss5   | 1783    | 2.363   | 34.592  | 1.271    | 36.548400   | -122.542593  |
| Nautiloe sp.        | 23 March 2017      | KOK2017-BW22 | 30   | NA     | NA     | NA     | 20.756111   | -157.255833  |
| Paraphyllina sp.    | 27 May 2019        | D0026 ss8 | 2385    | 1.858   | 34.592  | 1.943    | 36.116665   | -122.75     |
| Paraphyllina sp.    | 9 March 2015       | D0723 ss10 | 651    | 6.199   | 34.512  | 0.025    | 25.442516   | -109.852324  |
| Paraphyllina sp.    | 18 November 2019   | D1221 D12 | 2088    | 2.006   | 34.815  | 1.851    | 36.545798   | -122.538197  |
| Periphyllopsis sp.  | 27 February 2015   | D0715 ss1 | 1761    | 2.839   | 34.819  | 1.087    | 28.182585   | -119.599956  |
| Periphylla periphylla | 1 July 2015      | D0780 D11 | 534     | 5.231   | 34.169  | 0.433    | 36.15082    | -124.2852    |
| Periphylla periphylla | 15 November 2015  | D1218 ss12 | 384    | 7.542   | 34.158  | 0.996    | 36.695557   | -122.004649  |
| Periphylla periphylla | 15 November 2015  | D1218 ss6  | 392     | 6.940   | 34.184  | 0.763    | 36.698180   | -122.010072  |
| Periphylla periphylla | 16 November 2015  | D1219 D10 | 923     | 4.237   | 34.416  | 0.321    | 36.544387   | -122.537005  |

Table A2. Potential diagnostic trait table for species identification of *Atolla* based on existing keys [8–11] as well as original descriptions and our observations. Potential valid diagnostic traits are highlighted in yellow and we have grouped *A. tenella* with *A. aff. tenella* and *A. wyvillei* with *A. aff. wyvillei* as the molecular analysis shows that they are similar (Appendix A Table A3). Septa shape (divergent or straight), degree of extension into coronal muscle, and gonad shape are not considered by us to be valid diagnostic traits.

| Species       | A. chuni * | A. parva | A. vanhoeffeni | A. tenella and A. aff. tenella | A. gigantea | A. wyvillei and A. aff. wyvillei | A. reynoldsi sp. nov. | Atolla species A—tall, rounded dome | Atolla species B—White, very flat |
|---------------|------------|----------|----------------|-------------------------------|-------------|---------------------------------|----------------------|-----------------------------------|-----------------------------------|
| Pigment spots | No         | No       | Yes 2 per quadrant | Yes? 2 per tentacle a | No         | No                             | No                   | No                                | No                                |
| Papillae      | Yes        | No       | No             | No                            | No         | No                             | No                   | Yes, varies b                      | No                                |
| Ridges with spikes on rhopalia | No         | No       | No             | No                            | No         | No                             | Yes                  | No                                | No                                |
| Stomach       | Clover shaped | Clover shaped | Cross shaped | Clover shaped | Clover shaped | Clover shaped | Greek-cross shaped | Greek-cross shaped—evaginated | 59–64                            |
| Tentacles     | 24         | Yes      | 18–24          | 18–20                         | 22–30       | Yes                            | Yes                  | 26–39 coiled                      | No                                |
| Trailing tentacle | Yes      | Yes      | Yes            | Yes                           | Yes        | Yes                            | No                   | No                                | No                                |
### Table A2. Cont.

| Species | A. chuni * | A. parva | A. vanhoeffeni | A. tenella and A. aff. tenella | A. gigantea | A. wyvillei and A. aff. wyvillei | A. reynoldsi sp. nov. | Atolla species A—tall, rounded dome | Atolla species B—White, very flat |
|---------|------------|----------|----------------|--------------------------------|------------|---------------------------------|---------------------|---------------------------------|---------------------------------|
| Septa path c | ? | Straight or slightly divergent, club shaped | Straight | Divergent in description; straight in our specimens | Divergent (preserved look straight) | Divergent | Straight or slightly divergent | Straight |
| Septa extend to muscle d | ? | Yes | No | No | Yes | Yes e | Yes | Yes |
| Gonad shape f | Oval/bean | oval | Horseshoe | Circular with irregular edges | Horseshoe | Oval to large auricular | Oval but horseshoe shaped when mature | Horseshoe | Immature, horseshoe |

Footnotes: * not observed or collected in this study; ! Pigment spots not observed in our specimen or photos of A. tenella; b. Papillae in Atolla sp. B vary from a few solitary papilla to two rows of papillae on the rhopalia, loss of papillae may be a result of fixation; c. Path of the septa is not a good trait, as it is somewhat arbitrary and changes with preservation; d. Septa extending into coronal muscle is also not a robust trait; e. Septa not extending into coronal muscle is supposed to be diagnostic for A. wyvillei, but they do extend into the muscle; f. Gonads change shape as they mature, going from a C-shaped outline to oval and then to fully folded horseshoe. Other species in the literature: A. russelli—might have a Greek-cross shaped gut; A. bairdi—Smithsonian holotype photo online, looks like A gigantea (22 tentacles, divergent septa); A. verrilli—28 tentacles, straight septa—doubtful species, sometimes considered a synonym of A. wyvillei; A. valdiviae—doubtful species, sometimes considered a synonym of A. wyvillei. ? refers to unknown status as we have not observed a specimen of A. chuni.

### Table A3. Fixed differences for each Atolla species for COI barcode sequence (shaded in gray). Position refers to base pair position in alignment with A. wyvillei (GQ120088).

| COI mtDNA | Position |
|-----------|----------|
| Species   | 5  | 8  | 11 | 14 | 17 | 20 | 23 | 26 | 29 | 32 | 35 | 38 | 41 | 44 | 47 | 50 | 53 | 56 | 59 | 62 | 65 | 68 | 71 | 74 | 77 | 80 | 83 | 86 | 89 | 92 | 95 | 98 | 101 | 104 | 107 | 110 | 113 |
| Atolla sp. B | G  | T  | T  | T  | C  | A  | A  | A  | T  | A  | A  | T  | A  | A  | A  | T  | A  | C  | A  | A  | T  | A  | T  | T  | A  | A  | A  | A  | T  | A  | C  | A  | A  | A  |
| A. gigantea | A  | T  | T  | T  | A  | A  | T  | T  | A  | T  | A  | A  | T  | A  | A  | T  | T  | T  | T  | A  | T  | C  | T  | T  | A  | A  | C  | A  | T  | A  | C  | A  |
| A. reynoldsi | A  | G  | C  | C  | T  | C  | C  | C  | C  | T  | G  | G  | T  | A  | G  | G  | T  | T  | A  | T  | A  | G  | G  | G  | C  | A  | G  |
| A. parva | A  | T  | T  | T  | A  | T  | T  | A  | A  | T  | A  | A  | A  | A  | T  | T  | A  | T  | A  | T  | T  | T  | T  | T  | A  | A  | A  | A  | T  | A  | T  | A  | A  |
| A. aff. tenella | A  | T  | T  | T  | G  | A  | T  | T  | T  | A  | A  | T  | A  | A  | T  | T  | T  | T  | G  | T  | T  | T  | T  | T  | T  | A  | A  | A  | A  | T  | A  | A  | A  |
| A. tenella | A  | T  | T  | T  | T  | A  | T  | T  | T  | A  | C  | A  | A  | T  | A  | A  | C  | T  | G  | T  | A  | T  | T  | T  | T  | A  | A  | A  | A  | T  | A  | A  | A  |
| A. vanhoeffeni | A  | T  | T  | T  | G  | T  | C  | T  | T  | A  | A  | A  | A  | T  | A  | A  | T  | T  | T  | T  | A  | T  | A  | T  | A  | C  | A  | A  | A  | T  | A  | T  | A  |
| A. aff. wyvillei | A  | T  | T  | T  | T  | A  | T  | T  | T  | A  | T  | A  | A  | T  | A  | A  | T  | T  | T  | T  | T  | T  | T  | T  | A  | A  | A  | A  | T  | A  | T  | A  | A  |
| A. wyvillei | A  | T  | T  | T  | A  | A  | T  | T  | T  | A  | T  | A  | A  | A  | C  | T  | T  | T  | A  | T  | C  | T  | T  | A  | C  | A  | A  | A  | T  | A  | T  | A  | A  |
| COI cont. | Position |
|----------|----------|
| Species | 224 | 225 | 226 | 227 | 228 | 229 | 230 | 231 | 232 | 233 | 234 | 235 | 236 | 237 | 238 | 239 | 240 | 241 | 242 | 243 | 244 | 245 | 246 | 247 | 248 | 249 | 250 | 251 | 252 | 253 | 254 | 255 | 256 | 257 | 258 | 259 | 260 | 261 | 262 | 263 | 264 | 265 | 266 | 267 | 268 | 269 | 270 | 271 | 272 | 273 | 274 | 275 | 276 | 277 | 278 | 279 | 280 | 281 | 282 | 283 | 284 | 285 | 286 | 287 | 288 | 289 | 290 | 291 | 292 | 293 | 294 | 295 | 296 | 297 | 298 | 299 | 300 | 301 | 302 | 303 | 304 | 305 | 306 | 307 | 308 | 309 | 310 | 311 | 312 | 313 | 314 | 315 | 316 | 317 | 318 | 319 | 320 | 321 | 322 | 323 | 324 | 325 | 326 | 327 | 328 | 329 | 330 | 331 | 332 | 333 | 334 | 335 | 336 | 337 | 338 | 339 | 340 | 341 | 342 | 343 | 344 | 345 | 346 | 347 | 348 | 349 | 350 | 351 | 352 |
| Atolla sp. B | T | T | A | T | A | A | C | A | T | A | A | T | A | A | C | C | T | T | C | A | T | G | T | A | T | T | T |
| A. gigantea | T | T | A | C | A | A | T | T | T | A | T | A | T | T | T | T | T | C | A | T | G | T | T | T | T | T | T |
| A. reynoldsi | T | C | G | T | G | T | T | C | C | T | G | A | T | G | T | T | T | A | A | T | G | T | T | T | T | T | T |
| A. parva | T | T | A | C | C | A | T | T | T | A | T | T | A | T | T | T | T | A | T | G | T | T | T | T | T | T | T |
| A. aff. tenella | T | T | A | C | C | A | T | T | T | A | T | T | A | T | T | T | C | A | T | G | T | C | C | T | T |
| A. tenella | T | T | A | C | T | A | T | T | T | A | T | T | A | A | T | T | A | T | G | T | C | T | T | A | T |
| A. vanhoeffeni | C | T | A | C | A | A | T | C | T | A | T | A | A | T | T | T | T | A | A | T | T | A | T | A | T |
| A. aff. wyvillei | T | T | A | C | C | A | T | T | T | T | A | A | T | G | T | T | T | A | T | G | T | T | T | T | T | T |
| A. wyvillei | T | T | A | C | A | A | T | T | T | A | T | A | T | T | C | A | T | G | C | T | T | T | T | T | T | T |

| COI cont. | Position |
|----------|----------|
| Species | 358 | 361 | 364 | 367 | 370 | 371 | 372 | 373 | 374 | 375 | 376 | 377 | 378 | 379 | 380 | 381 | 382 | 383 | 384 | 385 | 386 | 387 | 388 | 389 | 390 | 391 | 392 | 393 | 394 | 395 | 396 | 397 | 398 | 399 | 400 | 401 | 402 | 403 | 404 | 405 | 406 | 407 | 408 | 409 | 410 | 411 | 412 | 413 | 414 | 415 | 416 | 417 | 418 | 419 | 420 | 421 | 422 | 423 | 424 | 425 | 426 | 427 | 428 | 429 | 430 | 431 | 432 | 433 | 434 | 435 | 436 | 437 | 438 | 439 | 440 | 441 | 442 | 443 | 444 | 445 | 446 | 447 | 448 | 449 | 450 | 451 | 452 | 453 | 454 | 455 | 456 | 457 | 458 | 459 | 460 | 461 | 462 | 463 | 464 | 465 | 466 | 467 | 468 | 469 | 470 | 471 | 472 | 473 | 474 | 475 | 476 | 477 | 478 | 479 | 480 | 481 | 482 | 483 | 484 | 485 | 486 | 487 | 488 | 489 | 490 | 491 | 492 | 493 | 494 | 495 | 496 | 497 | 498 | 499 | 500 | 501 | 502 |
| Atolla sp. B | A | T | A | T | A | A | T | T | T | T | T | T | T | T | C | T | T | A | A | T | A | C | A | A | C | T | T |
| A. gigantea | T | A | A | C | G | T | A | T | T | A | A | G | T | T | A | A | A | A | T | T | T | A | A | T | A | C | A |
| A. reynoldsi | T | A | G | T | G | C | C | T | A | A | C | C | A | A | C | T | G | G | C | G | T | C | T | C | C | A |
| A. parva | T | A | T | G | T | G | A | T | A | A | G | T | T | A | A | A | A | A | T | T | A | A | G | T | C | A | A | C | A |
| A. aff. tenella | T | A | A | T | G | C | A | T | T | A | A | G | T | T | A | A | A | A | T | T | A | A | G | T | C | A | A | C | A |
| A. tenella | T | A | A | T | G | C | A | T | T | A | A | G | T | T | A | A | A | A | T | T | A | A | G | T | C | A | A | C | A |
| A. vanhoeffeni | T | A | A | T | G | C | A | T | T | A | A | G | A | T | A | A | A | A | T | T | A | A | T | G | C | A | A | C | A |
| A. aff. wyvillei | T | A | A | T | G | C | A | T | T | C | A | A | C | T | A | A | A | A | T | T | A | A | T | G | C | A | A | C | A |
| A. wyvillei | T | A | A | T | G | T | A | T | A | A | G | T | T | A | A | A | A | T | T | A | A | T | A | C | A | A | C | A | A | C | A |
| COI cont. | Position |
|-----------|----------|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** |
| Atolla sp. B | A | T | A | T | T | T | A | G | T | T | A | T | T | T | A | T | T | A | T | G | T | A |
| A. gigantea | T | T | A | G | A | T | A | G | T | C | T | T | A | A | A | A | G | C | A | A | T | T | C | T | A | T |
| A. reynoldsi | T | C | T | G | C | C | G | G | A | C | T | T | A | G | A | T | G | A | C | T | T | G | A | G | C | C | G | C | T |
| A. parva | C | T | A | A | T | T | A | G | T | T | T | T | T | T | T | T | A | T | A | G | C | A | A | T | T | T | T | T |
| A. aff. tenella | T | T | A | A | A | T | A | G | T | C | T | T | T | G | A | A | A | A | G | C | A | A | T | T | T | T | A | C |
| A. tenella | T | T | A | A | T | T | A | G | T | C | T | T | T | T | T | T | A | T | A | A | G | C | A | A | T | T | T | C | T | A | T |
| A. vanhoeffeni | T | T | A | A | A | T | A | A | C | C | T | T | T | T | A | A | A | A | G | C | A | A | T | T | T | T | T | A | C | T | G |
| A. aff. wyvillei | C | T | A | A | T | T | A | G | T | C | T | T | T | T | A | T | A | A | A | G | C | A | A | T | T | T | T | T | T | T | T |
| A. wyvillei | T | T | A | A | T | T | A | G | T | C | T | T | T | T | T | T | A | A | A | A | G | C | A | A | T | T | T | C | T | A | T |

| COI cont. | Position |
|-----------|----------|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** |
| Atolla sp. B | T | T | G | A | T | T | A | A | C | T | A | A | A | A | T | T | T | T | G | G | T | T | A |
| A.gigantea | T | T | A | A | A | T | T | T | T | A | G | A | T | A | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T |
| A. reynoldsi | C | C | T | G | T | C | T | T | T | C | G | G | T | T | A | C | T | T | C | T | A | C | C | T |
| A. parva | T | T | C | T | T | T | T | T | A | T | T | T | A | G | G | T | A | T | T | T | T | T | T | T | T | T | C | T | A | C |
| A. aff. tenella | T | T | C | T | T | T | T | T | A | T | T | T | A | A | A | A | G | C | A | A | T | T | T | T | T | T | T | T | T | T | T |
| A. tenella | T | T | C | T | T | T | T | T | A | A | A | A | G | A | T | A | C | T | T | T | T | T | T | T | T | T | T | T | T | T | T |
| A. vanhoeffeni | T | T | T | T | T | T | A | T | T | T | A | G | A | T | A | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T |
| A. aff. wyvillei | T | T | C | T | T | T | T | T | A | A | A | A | G | A | T | A | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T |
| A. wyvillei | T | T | A | C | T | T | T | T | A | A | A | A | G | A | T | A | T | T | T | T | T | T | T | T | T | T | T | T | T | T | T |
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