



A new subfamily of ulmarid scyphomedusae, the Santjordiinae, with a description of *Santjordia pagesi* gen. et sp. nov. (Cnidaria: Scyphozoa: Discomedusae: Semaestomeae: Ulmaridae) from the Sumisu Caldera, Ogasawara Islands, Japan

DHUGAL JOHN LINDSAY^{1*}, MARY MATILDA GROSSMANN^{2,3}, JAVIER MONTENEGRO¹ & ANDRÉ CARRARA MORANDINI^{4,5}

¹Institute for Extra-cutting-edge Science and Technology Avant-garde Research (X-star), Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Kanagawa, Japan

✉ dhugal@jamstec.go.jp; <https://orcid.org/0000-0002-8985-4744>

✉ jmontalez@gmail.com; <https://orcid.org/0000-0002-0289-3274>

²Okinawa Institute of Science and Technology (OIST), Onna, Okinawa, Japan

✉ grossmann.mary@gmail.com; <https://orcid.org/0000-0002-6800-6092>

⁴Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, n. 101, São Paulo, SP, Brazil, 05508-090

✉ acmorand@ib.usp.br; <https://orcid.org/0000-0003-3747-8748>

⁵Centro de Biologia Marinha (CEBIMar), Universidade de São Paulo, Rod. Manoel Hipólito do Rego, km 131.5, São Sebastião, SP, Brazil, 11612-109

*Corresponding author

Abstract

An undescribed species of ulmarid medusa was observed *in situ* and captured at 812 m depth within the Sumisu Caldera, Ogasawara Islands, Japan. Morphological and molecular evidence points to it being distinct from other ulmarid medusae and a new species (*pagesi*), genus (*Santjordia*) and subfamily (Santjordiinae) are herein erected to contain it. This new subfamily of semaeostome ulmarid medusae has both marginal and subumbrellar rhopalia, making it unique within the order Semaestomeae. Although the combination of subumbrellar tentacles and the lack of branched canals should warrant the erection of a new family within the Semaestomeae, a lack of information on the gonad structure and poor bootstrap support in the molecular phylogenetic tree cause us to relegate it to the catch-all family Ulmaridae, until greater taxon sampling and phylogenetic analyses are carried out for the Semaestomeae.

Key words: deep sea, medusa, new species, new genus, submarine caldera

Introduction

Scyphomedusae are among the largest and most robust members of the gelatinous zooplankton (Cornelius 1997a) and, whereas a considerable percentage of the gelatinous fauna is damaged beyond easy recognition in traditional sampling devices such as midwater trawls and nets, it could be expected that the Scyphomedusae would be one of the better-characterized groups, due to their greater physical robustness associated with lower water content than in other Medusozoa (Lucas *et al.* 2011). In shallow waters, where sampling with dip nets or by scuba divers allows the collection of pristine specimens, a combination of careful morphological studies and the application of molecular techniques has led to the description or resurrection of a number of species (*e.g.*, Dawson 2005; Gershwin & Zeidler 2008; Morandini & Marques 2010; Nishikawa *et al.* 2014; Piraino *et al.* 2014; Avian *et al.* 2016; Scorrano *et al.* 2017). Molecular studies suggest that there is a great deal of cryptic diversity within this group (*e.g.*, Dawson & Jacobs 2001; Appeltans *et al.* 2012). Traditional systematics counts 218 (Daly *et al.* 2007) to 223 (Jarms & Morandini 2019) species, but estimates suggest that the diversity of the class could reach 338–383 species (Appeltans *et al.* 2012). By comparison, our knowledge of the diversity of deep-sea forms is extremely limited. However, the use

of crewed submersibles and unmanned remotely-operated vehicles (ROVs) has allowed the discovery, in deep waters, of at least two new species in two new subfamilies of quite large semeanostome medusae (Matsumoto *et al.* 2003; Raskoff & Matsumoto 2004). Semeanostomeae currently contains five families (Collins *et al.* 2022), with two being monogeneric (Drymonematidae, Phacellophoridae), one containing two genera (Cyaneidae), and one containing four genera (Pelagiidae). The remaining family, Ulmaridae, contains thirteen genera! These genera are presently contained within eight subfamilies, six of them monogeneric (Jarms & Morandini 2019) and five of them containing only deep-sea species. The large size and fragility of these deep-sea taxa have undoubtedly contributed to the situation where not enough material is available in good condition to assess intra-species and intra-generic differences in morphology, though large morphological differences point clearly to the presence of many higher-level taxa.

This manuscript describes a large, enigmatic, but easily recognizable medusa from yet another new subfamily within the Family Ulmaridae Haeckel, 1880—a family that appears to be much more diverse within the deep sea than had previously been supposed, and which is ripe for a taxonomic revision.

Materials and Methods

A single specimen was captured by the ROV *Hyper-Dolphin* during a cruise by the R/V *Kaiyo* (KY02-03) to the Ogasawara Island Chain, south of the Japanese mainland. It was captured using a gate valve sampler (Fig. 1; Lindsay 2003; Lindsay *et al.* 2004; Lindsay 2022a) after being filmed using the ROV's HDTV camera (specifications in Lindsay *et al.* 2008). A second individual was observed, but not captured (Lindsay 2022b). Physico-chemical data were collected using a SeaBird SBE19 CTD (Conductivity Temperature Depth meter) and an SBE43 oxygen sensor attached to the vehicle (Hidaka *et al.* 2021). It was also photographed within the gate valve sampler in the ship laboratory using a Nikon D1H digital camera with a macro lens (AF Micro Nikkor 105mm 1:2.8 D) and recorded in JPEG format at an image size of 2000 x 1312 pixels (Lindsay 2022c). Illumination was provided by National Ref Lamp colour-balanced flood bulbs (PRF-500WB), which lit the specimen from the side before a black felt backdrop.

A tentacle was cut off and preserved in 99.5% ethanol for subsequent DNA analyses and the remainder of the animal was preserved in buffered 5% formalin-seawater solution. Line drawings were made by tracing from photographs of the living specimen using Adobe Illustrator v5.1 supplemented by observations under a Leica MZ16 dissecting scope. A nematocyst slide squash was prepared from a formalin-preserved tentacle to identify nematocyst composition (Lindsay 2022d).

Other “Semeanostomeae” samples were collected from various geographic locations (Table 1, Lindsay *et al.* 2022e–k), identified on board, preserved in 99.5% ethanol and stored at -20°C until analysis. For all but *Deepstaria enigmatica* and *Tiburonia granrojo*, DNA extraction, amplification and sequencing of the 16S mitochondrial rDNA gene were performed following the protocol established in Collins *et al.* (2008). For *D. enigmatica* and *T. granrojo*, total DNA was extracted using the Qiagen (Valencia, California, USA) DNeasy Blood & Tissue Kit, and a 623 bp segment of the mitochondrial 16S gene was amplified and sequenced using ‘primer 1’ (5'-3' TCGACTGTTTACCAAAAACATAGC) and ‘primer 2’ (5'-3' ACGGAATGAACTCAAATCATGTAAG) from Cunningham & Buss (1993) with the TaKaRa (Otsu, Shiga, Japan) ExTaq and BigDye kits. Sequencing was performed on an ABI 3130xl sequencer. The 16S rDNA sequence for each sample was established as the consensus of the forward and reverse reads and deposited on GenBank (Table 1). An additional 48 sequences from GenBank were added to the analysis (Table 2). This resulted in a final dataset that included 38 sequences of “Semeanostomeae”, 21 sequences of “Rhizostomeae”, and two cubozoans.

All 16S-rDNA sequences, those newly generated and downloaded from GenBank, were aligned using Geneious Prime 2022.1.1. (<https://www.geneious.com>). A preliminary alignment was done with the Geneious alignment tool employing the “Global alignment with free end gaps” settings. This preliminary alignment was manually trimmed and thereafter realigned within Geneious using MAFF v7.450 (Kato and Standley 2013) with the algorithm L-INS-I and default settings. The resulting alignment was manually curated, and automatically edited with GBlock (Castresana 2000) allowing for small blocks, gap positions within blocks and flanking positions; this was done in order to preserve the phylogenetic signal from indels in the 16S-rDNA.

TABLE 1. Scyphozoan specimens examined morphologically and sequenced (16S) for the present work.

Species	16S Accession No.	Sequence ID	Sample ID	Image Vouchers	Cruise	Date	Depth (m)	Sampling location		
								Lat.	Long.	Location
<i>Deepstaria enigmatica</i>	ON391156	DLSI014	HD98SS1a (NSMT-Co 1404)	doi 10.5281/zenodo.6475523 doi 10.5281/zenodo.6480763	R/V Kaiyo, KY02-06	22-Apr-2002	669	41°00'N	144°41'E	Japan Trench
<i>Desmonema glaciale</i>	ON391153	DLSI110	UM12_RMT200_Dg	doi 10.5281/zenodo.6471770	TRV Umitaka Maru, CEAMARC	10-Feb-2008	0–200	66°35.5'S	144°1.5'E	Southern Ocean
<i>Des. glaciale</i>	ON391152	DLSI126	UM42_IYGPT500_Dg	n.a.	TRV Umitaka Maru, CEAMARC	6-Feb-2008	0–500	66°19.8'S	140°02.3'E	Southern Ocean
<i>Diplulmaris antarctica</i>	ON391163	DLSI116	UM25_RMT-S-8-2_Da	n.a.	TRV Umitaka Maru, CEAMARC	7-Feb-2008	50–100	66°20'S	141°22'E	Southern Ocean
<i>Pelagia noctiluca</i>	ON391151	DLSI223	RHB_MOC-1-2-7_Pn	n.a. (1.5 cm diameter)	R/V Ronald H. Brown, RHB06-03	16-Apr-2006	25–50	29°55'N	70°03'W	Caribbean Sea
<i>Poralia rufescens</i>	ON391159	DLSI070	UM16_RMT-D-8-2_Pr	n.a.	TRV Umitaka Maru, CEAMARC	31-Jan-2008	500–1000	63°S	140°E	Southern Ocean
<i>Po. rufescens</i>	ON391161	DLSI114	UM17_RMT-D-8-1_Pr	doi 10.5281/zenodo.6471820	TRV Umitaka Maru, CEAMARC	29-Jan-2008	500–1000	63°30.1'S	139°59.8'E	Southern Ocean
<i>Po. rufescens</i>	ON391162	DLSI311	2K1201SS4b_Pr_juv	doi 10.5281/zenodo.6472194	R/V Natsushima, NT00-08-3	6-Jul-2000	1136	35°09'N	139°13.656'E	Sagami Bay, Japan
<i>Po. rufescens</i>	ON391160	DLSI221	RHB_MOC-10-1-4_Pr	n.a.	R/V Ronald H. Brown, RHB06-03	15-Apr-2006	1000–3000	33°40'N	69°30'W	Caribbean Sea
<i>Sanfjordia pagesi</i> sp. nov.	ON391158	DLSI063	HD84GS1a	doi 10.5281/zenodo.6426355 doi 10.5281/zenodo.6420570 doi 10.5281/zenodo.6424652	R/V Kaiyo Cruise KY02-03	10-Mar-2002	789	31°28.3'N	140°04'E	Sumisu Caldera, Japan
<i>Syngomedusa gigantea</i>	ON391154	DLSI035	UM15_RMT-D-8-2_Sg	n.a.	TRV Umitaka Maru, CEAMARC	30-Jan-2008	200–500	62°31.3'S	139°58.5'E	Southern Ocean
<i>St. gigantea</i>	ON391155	DLSI163	UM14_IYGPT500_Sg	doi 10.5281/zenodo.6471790	TRV Umitaka Maru, CEAMARC	29-Jan-2008	0–500	62°1.5'S	140°2.5'E	Southern Ocean
<i>Tiburonia gramajo</i>	ON391157	DLSI004	HD98SS1a (NSMT-Co 1405)	doi 10.5281/zenodo.6476641	R/V Kaiyo, KY02-06	23-Apr-2002	986	41°00'N	144°42'E	Japan Trench

n.a.—not available.

TABLE 2. Scyphozoan sequences of the 16S-rDNA mitochondrial gene downloaded from GenBank.

Class	Order	Family	Genus	Species	GenBank
Scyphozoa	Semaeostomae	Drymonematidae	<i>Drymonema</i>	<i>Drymonema larsoni</i>	HQ234632
Scyphozoa	Semaeostomae	Drymonematidae	<i>Drymonema</i>	<i>Drymonema larsoni</i>	HQ234651
Scyphozoa	Semaeostomae	Drymonematidae	<i>Drymonema</i>	<i>Drymonema</i> sp.1	KY610743
Scyphozoa	Semaeostomae	Drymonematidae	<i>Drymonema</i>	<i>Drymonema dalmatinum</i>	HQ234634
Scyphozoa	Semaeostomae	Pelagiidae	<i>Pelagia</i>	<i>Pelagia noctiluca</i>	EU999227
Scyphozoa	Semaeostomae	Pelagiidae	<i>Pelagia</i>	<i>Pelagia noctiluca</i> DLSI223	NEW
Scyphozoa	Semaeostomae	Pelagiidae	<i>Chrysaora</i>	<i>Chrysaora fuscescens</i>	JX393256
Scyphozoa	Semaeostomae	Pelagiidae	<i>Chrysaora</i>	<i>Chrysaora helvola</i>	JX393257
Scyphozoa	Semaeostomae	Pelagiidae	<i>Chrysaora</i>	<i>Chrysaora quinquecirrha</i>	JX393259
Scyphozoa	Semaeostomae	Pelagiidae	<i>Chrysaora</i>	<i>Chrysaora melanaster</i>	JX393258
Scyphozoa	Semaeostomae	Pelagiidae	<i>Mawia</i>	<i>Mawia benovici</i>	KM217210
Scyphozoa	Semaeostomae	Pelagiidae	<i>Sanderia</i>	<i>Sanderia malayensis</i>	AB720911
Scyphozoa	Semaeostomae	Pelagiidae	<i>Chrysaora</i>	<i>Chrysaora</i> sp.	JN184787
Scyphozoa	Semaeostomae	Cyaneidae	<i>Cyanea</i>	<i>Cyanea</i> sp.	JX393244
Scyphozoa	Semaeostomae	Cyaneidae	<i>Cyanea</i>	<i>Cyanea</i> sp.	JX393270
Scyphozoa	Semaeostomae	Cyaneidae	<i>Cyanea</i>	<i>Cyanea capillata</i>	AB720912
Scyphozoa	Semaeostomae	Cyaneidae	<i>Cyanea</i>	<i>Cyanea</i> sp.	JX393225
Scyphozoa	Semaeostomae	Cyaneidae	<i>Desmonema</i>	<i>Desmonema glaciale</i> DLSI126	NEW
Scyphozoa	Semaeostomae	Cyaneidae	<i>Desmonema</i>	<i>Desmonema glaciale</i> DLSI110	NEW
Scyphozoa	Semaeostomae	Cyaneidae	<i>Desmonema</i>	<i>Desmonema</i> sp.	KY610740
Scyphozoa	Semaeostomae	Ulmaridae	<i>Aurelia</i>	<i>Aurelia limbata</i>	AB720914
Scyphozoa	Semaeostomae	Ulmaridae	<i>Aurelia</i>	<i>Aurelia aurita</i>	MH064432
Scyphozoa	Semaeostomae	Ulmaridae	<i>Aurelia</i>	<i>Aurelia labiata</i>	JX393253
Scyphozoa	Semaeostomae	Ulmaridae	<i>Aurelia</i>	<i>Aurelia aurita</i>	U19373
Scyphozoa	Semaeostomae	Ulmaridae	<i>Stygiomedusa</i>	<i>Stygiomedusa gigantea</i> DLSI035	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Stygiomedusa</i>	<i>Stygiomedusa gigantea</i> DLSI163	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Deepstaria</i>	<i>Deepstaria enigmatica</i>	KY610680
Scyphozoa	Semaeostomae	Ulmaridae	<i>Deepstaria</i>	<i>Deepstaria enigmatica</i> DLSI014	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Tiburonia</i>	<i>Tiburonia granrojo</i> DLSI004	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Santjordia</i>	<i>Santjordia pagesi</i> sp. nov. DLSI063	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i> DLSI070	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i>	KY610659
Scyphozoa	Semaeostomae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i> DLSI221	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i> DLSI114	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i> DLSI311	NEW
Scyphozoa	Semaeostomae	Ulmaridae	<i>Diplulmaris</i>	<i>Diplulmaris antarctica</i> DLSI116	NEW
Scyphozoa	Semaeostomae	Phacellophoridae	<i>Phacellophora</i>	<i>Phacellophora camtschatica</i>	AB720915
Scyphozoa	Semaeostomae	Phacellophoridae	<i>Phacellophora</i>	<i>Phacellophora</i> sp.	JX393262
Scyphozoa	Rhizostomae	Stomolophidae	<i>Stomolophus</i>	<i>Stomolophus</i> sp.4	KY610651
Scyphozoa	Rhizostomae	Stomolophidae	<i>Stomolophus</i>	<i>Stomolophus</i> sp.3	KY610649
Scyphozoa	Rhizostomae	Stomolophidae	<i>Stomolophus</i>	<i>Stomolophus meleagris</i>	KY610636

...Continued on the next page

TABLE 2. (Continued)

Class	Order	Family	Genus	Species	GenBank
Scyphozoa	Rhizostomae	Rhizostomatidae	<i>Rhopilema</i>	<i>Rhopilema hispidum</i>	AB720917
Scyphozoa	Rhizostomae	Rhizostomatidae	<i>Rhopilema</i>	<i>Rhopilema verrilli</i>	JX393271
Scyphozoa	Rhizostomae	Rhizostomatidae	<i>Rhizostoma</i>	<i>Rhizostoma pulmo</i>	KY610632
Scyphozoa	Rhizostomae	Rhizostomatidae	<i>Rhopilema</i>	<i>Rhopilema esculentum</i>	EU373725
Scyphozoa	Rhizostomae	Rhizostomatidae	<i>Nemopilema</i>	<i>Nemopilema nomurai</i>	AB720926
Scyphozoa	Rhizostomae	Mastigiidae	<i>Mastigias</i>	<i>Mastigias</i> cf. <i>papua etpisoni</i>	KU901023
Scyphozoa	Rhizostomae	Mastigiidae	<i>Mastigias</i>	<i>Mastigias papua</i>	AB720919
Scyphozoa	Rhizostomae	Mastigiidae	<i>Phyllorhiza</i>	<i>Phyllorhiza punctata</i>	KY610625
Scyphozoa	Rhizostomae	Mastigiidae	<i>Phyllorhiza</i>	<i>Phyllorhiza pacifica</i>	KY610622
Scyphozoa	Rhizostomae	Cassiopeidae	<i>Cassiopea</i>	<i>Cassiopea mayeri</i>	MW164859
Scyphozoa	Rhizostomae	Cassiopeidae	<i>Cassiopea</i>	<i>Cassiopea frondosa</i>	MT709259
Scyphozoa	Rhizostomae	Lychnorhizidae	<i>Lychnorhiza</i>	<i>Lychnorhiza lucerna</i>	KY610591
Scyphozoa	Rhizostomae	Lobonemidae	Lobonematidae	Lobonematidae sp.3	KY610606
Scyphozoa	Rhizostomae	Lobonemidae	Lobonematidae	Lobonematidae sp.1	KY610603
Scyphozoa	Rhizostomae	Catostylidae	<i>Crambione</i>	<i>Crambione mastigophora</i>	KY610602
Scyphozoa	Rhizostomae	Catostylidae	<i>Catostylus</i>	<i>Catostylus</i> sp.	KT982719
Scyphozoa	Rhizostomae	Catostylidae	<i>Catostylus</i>	<i>Catostylus townsendi</i>	OK299144
Scyphozoa	Rhizostomae	Catostylidae	<i>Crambionella</i>	<i>Crambionella orsini</i>	KY610589
Cubozoa	Chirodropida	Chirodropidae	<i>Chironex</i>	<i>Chironex fleckeri</i>	GQ849103
Cubozoa	Carybdeida	Alatinidae	<i>Alatina</i>	<i>Alatina alata</i>	JN642338

The final alignment consisted of 61 sequences of 375 bp in length. jModelTest 2.1.10 v20160303 (Darriba *et al.* 2012) was used to search for the best fitting substitution model. Maximum likelihood (ML) and Bayesian posterior inference (BI) phylogenetic estimations were generated within Geneious using the GTR+I+G model. ML phylogeny was generated using RAxML v8.2.11 (Stamatakis 2014) with rapid bootstrapping and search for best-scoring tree with the options “ -f a -x 1 ”, 1000 bootstrap replicates and 12345 parsimony random seeds. BI phylogeny was constructed using MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003) with a chain length of 5,000,000, four heated chains with a temperature of 0.2, a subsampling frequency of 200, and a burn-in length of 25%, at which point the average standard deviation of split frequency was steady below 0.01. The sequences of cubozoans were used as the outgroups in both the ML and BI analyses.

The COXI gene was amplified and sequenced from *Santjordia pagesi* **gen. et sp. nov.** following the protocol established in Nishikawa *et al.* (2014), because of the frequent use of this marker in eDNA and barcoding analyses. However, because of the low resolution of this marker at higher taxa, no phylogenetic reconstructions were performed. Nevertheless, it was included as part of the species description of *Santjordia pagesi* **gen. et sp. nov.** (GenBank accession number ON496462).

Terminology for taxonomic characters is described in Figure 2. In line with Russell (1970), Cornelius (1997b), Mianzan & Cornelius (1999) and Jarms & Morandini (2019; Fig. 11), the mouth lips/stomach pouches/corners of the mouth (prolonged into the mouth-arms) are termed perradial, unlike the situation in *Aurelia* where the mouth-arms are perradial but the stomach pouches are interradian (Dawson 2003). Additional samples observed and sequenced are listed in Table 1. A list of sequences from GenBank used for the analysis can be found in Table 2.

The holotype [HD84GS1] was deposited at the Showa Memorial Institute, National Science Museum, Tokyo (NSMT-Co-1800).

Results

Systematics

Class Scyphozoa Goette, 1887

Order Semaestomeae L. Agassiz, 1862

Family Ulmaridae Haeckel, 1880

Subfamily Santjordiinae subfam. nov.

Genus *Santjordia* gen. nov.

Family Ulmaridae Haeckel, 1880 emend. Larson, 1986

Semaestomeae with central gastric cavity emitting peripherally radiating canals (either simple or branched) joining the marginal ring canal; oral arms either broad and curtain-like or narrow and tapering; lips usually with nematocyst-lined papillae or digitata; gonads either inverted or everted; tentacles either marginal, subumbrellar or absent.

Subfamily Santjordiinae subfam. nov.

New Japanese name: Sekijuujikurage-aka

Ulmaridae in which the tentacles arise in linear clusters from the subumbrella; without subgenital pits; marginal and subumbrellar rhopalia; with narrow, tapering oral arms.

Genus *Santjordia* gen. nov.

New Japanese name: Sekijuujikurage-zoku

Santjordiinae with bell margin divided into 8 broad velar lobes; subumbrellar tentacles in pits over ring canal (Figs. 3a–e, 4); four perradial canals wide, emanating from centre of distal tips of red, cross-shaped stomach base; four interr radial canals wide, unbranched (simple), emanating from angles between stomach pouches; eight adradial canals wide, emanating from corners of distal tips of stomach pouch base, not in direct communication with perradial nor interr radial canals; 32 rhopalia, the 24 adradial rhopalia protruding through circular perforations in the velar lobes (Fig. 3f) and supplied by rhopaliar canals emanating from the ring canal; 4 oral arms, with bases fused and following outline of cross-shaped stomach.

Etymology

The genus name *Santjordia* refers to the red cross of Saint George (Catalan: Sant Jordi)—the shape and colour of which correspond well to the distinctive stomach base in this genus and species. Saint George is also the patron saint of Catalonia, where the first author began the present work while on sabbatical in the laboratory of a Catalan taxonomist.

***Santjordia pagesi* sp. nov.**

(Figs. 1–5)

New Japanese name: Sekijuujikurage

Synonymy

“Ulmaridae **gen. et sp.**” Kitamura *et al.* 2008: 320, fig. 24.57.

“Ulmaridae **gen. et sp. nov.**” Hidaka *et al.* 2021: 52.

Holotype

NSMT-Co-1800—One specimen captured by the ROV *Hyper-Dolphin* during Dive 84 on 10 March 2002 at a depth of 812 m (temperature 10.2°C, salinity 34.30, dissolved oxygen 2.8 ml/L, Sigma T 26.37) within the hydrothermally active Sumisu Caldera (31°28'N 140°04'E) in the Izu-Ogasawara Islands south of the Japanese mainland. The reference video file (*in situ*) in the JAMSTEC High-quality Video Database is HPD0084-20020310-103457.9343-SHHD-Front-1920x1080_HDCAM-1o4--NoImpose-Santjordia_pagesi-Dhugal_Lindsay-SEKIJUUIKURAGE-812.9 m-20020310T013457.9343Z.mov and a transcoded “lightweight” version is accessible on Zenodo (Lindsay 2022a). Images taken in the shipboard laboratory within the gate sampler (Lindsay 2022c) and microscope images of tentacle squashes (Lindsay 2022d) are available online on Zenodo.

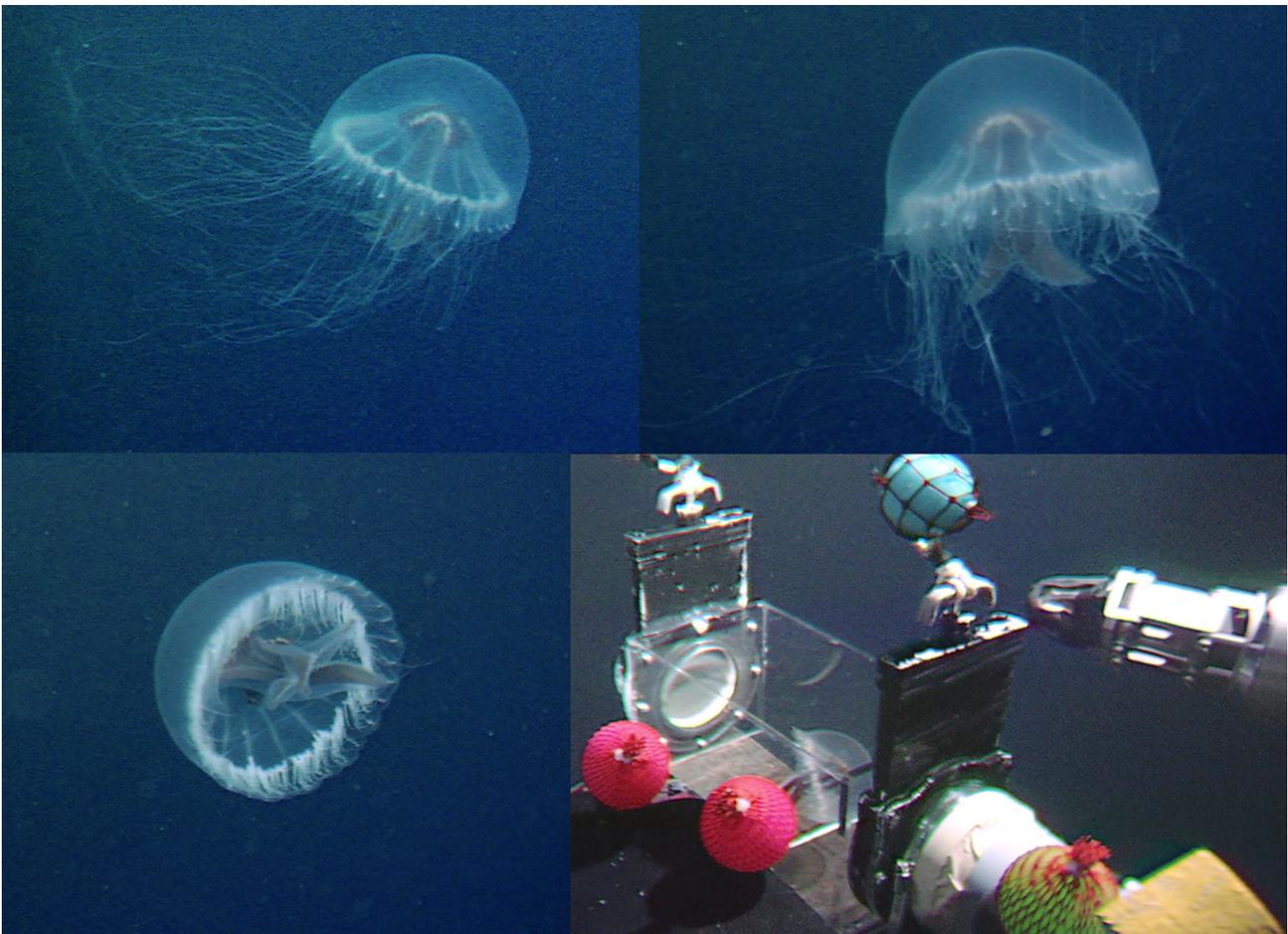


FIGURE 1. *In situ* images of the holotype of *Santjordia pagesi* **gen. et sp. nov.** Top left: aboral-lateral view; top right: lateral view; bottom left: oral-lateral view; bottom right: lateral view within the gate valve sampler on the ROV *Hyper-Dolphin*. Specimen size = 100 mm diameter.

Other Material

A second individual was observed at 843 m depth (temperature 10.1°C, salinity 34.35, dissolved oxygen 2.8 ml/L, Sigma T 26.43). The reference video file is HPD0084-20020310-105552-SHHD-Front-1920x1080_HDCAM-1o4-

Holotype Description

Umbrella hemispherical; 100 mm diameter, 72 mm height; scattered with nematocysts; mesoglea thick, transparent. Margin cleft into 8 broad lobes (lappets). Eight rhopalia (4 perradial, 4 interradial) located in clefts at margin; 24 additional adradial rhopalia located on the subumbrellar surface but protruding through tear-drop-shaped perforations in the velar lobes (3 per octant) (Figs 2, 3f). Tentacles subumbrellar; up to 60 per quadrant; located in pits in 2 rows along inner [proximal] and outer [distal] surfaces of ring canal; tentacle pits demarcated by rhopaliar canals and other less obvious subumbrellar gelatinous ridges; single tentacle at base of each adradial canal just proximal of where it joins ring canal, not in a pit; tentacle bases light pink when alive, cream in formalin. Tentacle nematocysts composed of small holotrichous a-isorhizas (average length $8.91 \pm 0.74 \mu\text{m}$, average width $5.09 \pm 0.42 \mu\text{m}$; range $7.3\text{--}11.0 \mu\text{m} \times 4.2\text{--}6.6 \mu\text{m}$; $n=95$) and heterotrichous microbasic birhopaloids (average length $11.63 \pm 0.98 \mu\text{m}$, average width $8.24 \pm 0.24 \mu\text{m}$; range $10.0\text{--}12.6 \mu\text{m} \times 7.8\text{--}8.5 \mu\text{m}$; $n=10$) (Fig. 5). Subumbrellar musculature not discernible. Subgenital ostia absent. Manubrium height equal to or slightly greater than bell radius; surrounded by thick transparent mesoglea with inner surface red-pigmented. Four V-shaped oral arms; bases fused and following outline of cross-shaped stomach; tips protruding below umbrella rim; with transparent papillae on tips and inner edges, thick transparent mesoglea extends to distalmost ends of oral arms, inner surfaces red-pigmented. Central stomach cross-shaped, red when alive, dark brown in formalin; gastric cirri in 4 pairs of perradial groups, whitish in live specimen; radial canals simple, not anastomosing, similar width throughout length, connected by a ring canal located $\sim 1/3$ bell radius away from margin; short rhopaliar canals emanating from ring canal to all sense organs; 4 perradial canals, one each emanating from centre of distal tips of stomach base; 4 interradial canals, one each emanating from centre of stomach base; 8 adradial canals, two each emanating from distal tips of stomach base, one at each corner, not in direct communication with perradial or interradial canals. Gonads not recognized.

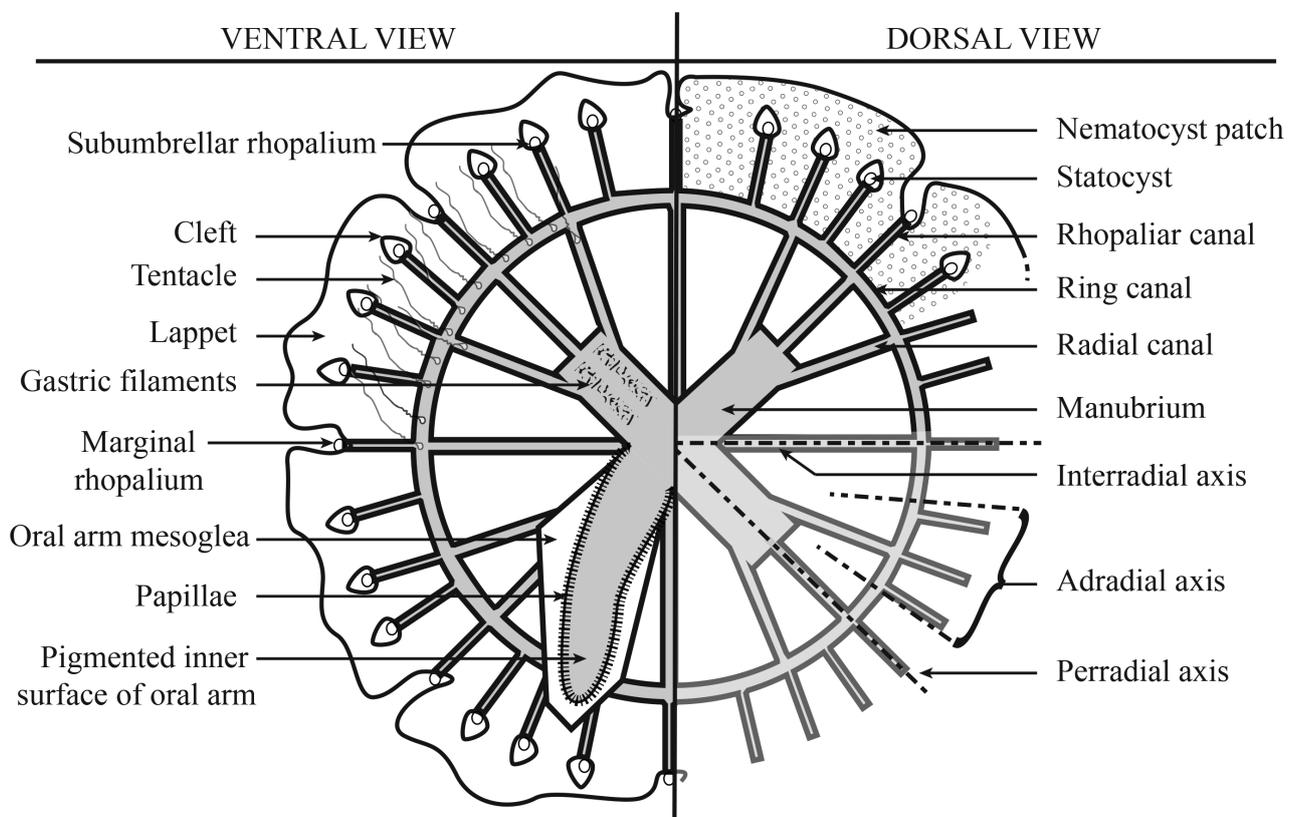


FIGURE 2. Schematic diagram of *Santjordia pagesi* **gen. et sp. nov.** with morphological terminology.

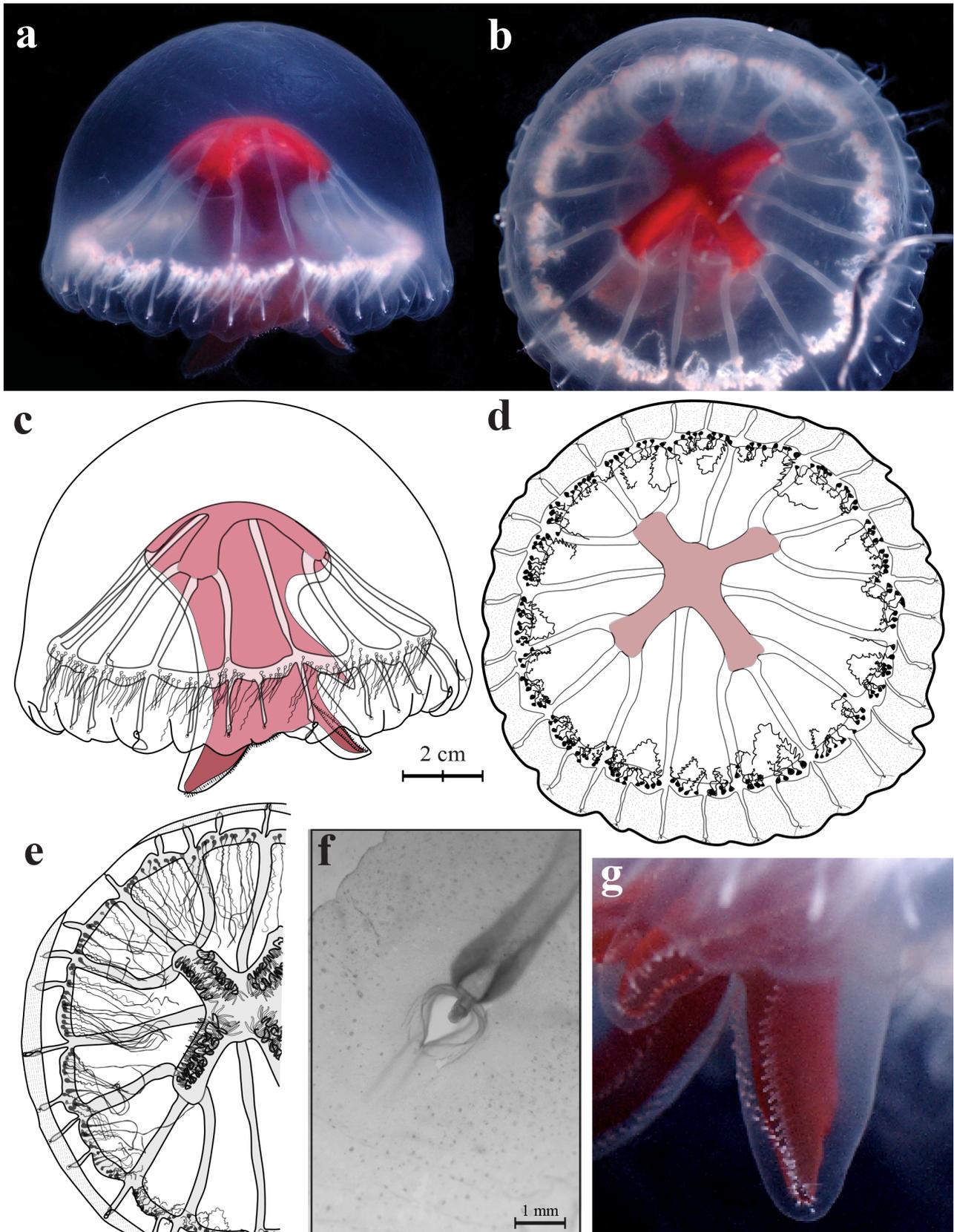


FIGURE 3. *Santjordia pagesi* gen. et sp. nov. Holotype. a: photograph of lateral view of living specimen in the gate sampler; b: photograph of aboral view of living specimen in the gate sampler; c: sketch of lateral view of living specimen; d: sketch of aboral view of living specimen; e: sketch of portion of oral view of preserved specimen; f: close-up of adradial rhopalium of preserved specimen, showing exumbrella with cleft, statocyst and rhopalial canal; g: close-up of oral arm of living specimen in the onboard aquarium, showing marginal papillae. Scale bar = 2 cm except f: scale bar = 1 mm.

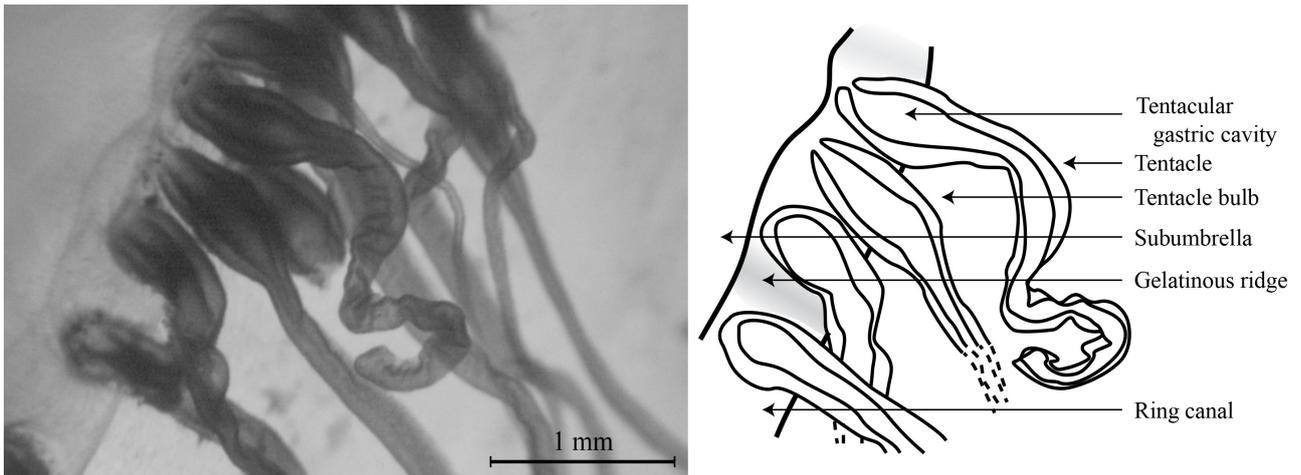


FIGURE 4. Close-up photograph of subumbrella of preserved specimen of *Santjordia pagesi* **gen. et sp. nov.** holotype showing tentacle disposition. Sketch of subumbrella photograph, labelled with morphological characters. Scale bar = 1 mm.

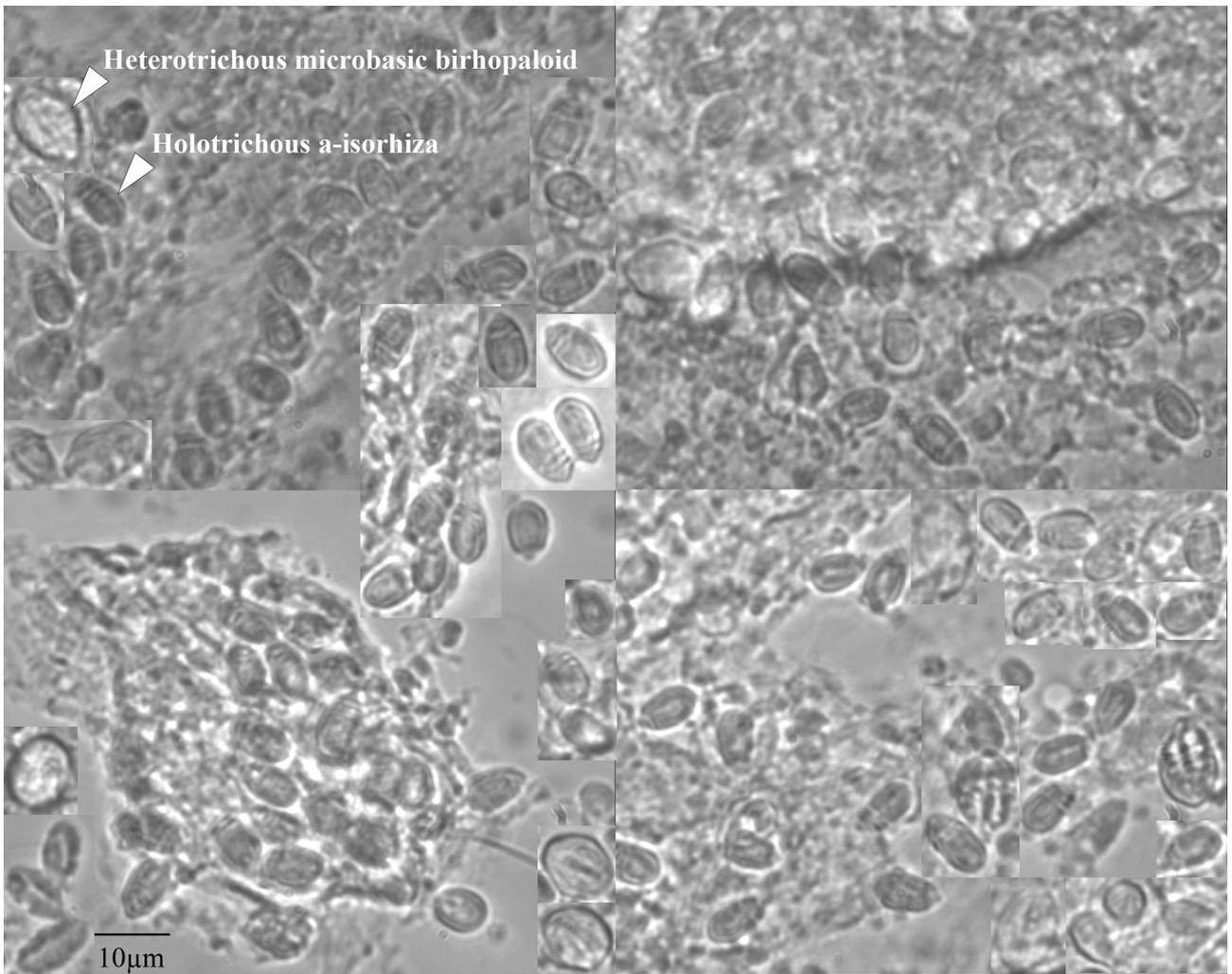


FIGURE 5. Photograph montage of a tentacle squash from the preserved specimen of *Santjordia pagesi* **sp. nov.** holotype showing nematocyst size and morphology. Scale bar = 10 µm.

Etymology

The species name is in honour of Dr. Francesc Pagès, who hosted the first author during his sabbatical in Barcelona and introduced him to the intricacies of cnidarian taxonomy.

Molecular Phylogeny

The analysis of sequences of the mitochondrial 16S gene using maximum likelihood (ML) and Bayesian methods gave congruent tree topologies (Fig. 6). Robust support was evident for the sennaeostome clades Drymonematidae and Cyaneidae, and for another clade including the ulmarid subfamilies Poraliinae and a member of the Ulmarinae, but also including the recently erected family Phacellophoridae. In fact, higher support was evident for *Diplulmaris* (Ulmarinae) and *Phacellophora* (Phacellophoridae) being more closely related to each other than for a close relationship between some of the ulmarid genera investigated. Somewhat surprisingly, there was reasonable support for *Santjordia pagesi* **gen. et sp. nov.** belonging to a sister group to a clade including the ulmarid subfamilies lacking marginal tentacles—Stygiomedusinae + Tiburoniinae + Deepstariinae. A BLAST search for the COXI sequence returned a maximum percentage identity of 82.62% with a query cover of 95% matched with *Aurelia coerulea*, with the next closest match being *Rhopilema* aff. *esculentum* at 82.21% and 97%, respectively. These low values are indicative of the COXI marker not being suitable for resolving higher phylogenies and further analysis was not attempted. Sequences determined in the present study have been registered on GenBank under accession numbers ON391151–ON391163 for 16S and ON496462 for the single COXI sequence, belonging to *Santjordia pagesi* **gen. et sp. nov.** All sequences used in the molecular analysis are listed in Tables 1 and 2. Images of sequenced specimens, where available, are available online on Zenodo (Lindsay 2022a–k).

Remarks

The medusa was swimming upwards at a pulse rate of 0.4 Hz at a depth of 812 m and an altitude of 101 m above the bottom. Only two individuals were observed over 91 minutes of observation time during descent below the caldera rim at 400 m depth inside the Sumisu Caldera, and no individuals were observed during a second dive during descent to a maximum depth of 893 m above the outer wall slope of the caldera on the previous day (31°29.1'N, 140°09.3'E; total observation time below 400 m: 115 min). Compared to environmental parameters outside the caldera in the open ocean, temperature at 812 m depth was elevated within the caldera (10.2°C vs 5.5 °C), as was the dissolved oxygen concentration (2.8 ml/L vs 1.7 ml/L). The oceanographic environment within the Sumisu Caldera is described and discussed in more detail by Hidaka *et al.* (2021). The caldera wall around this depth is comprised of monomictic lava breccia, coherent facies or talus blocks, while most of the caldera floor is covered with pumiceous sand and pebbles with some lobes of coarser debris (Tani *et al.* 2008). Other organisms observed in the same depth layer as *Santjordia pagesi* **gen. et sp. nov.** included the calycophoran siphonophore *Clausophyes* sp. (see Hidaka *et al.* 2021), pyrosomes (Pyrosomatidae spp.) (see Hidaka *et al.* 2021), euphausiids, sergestid shrimps, the hyperiid amphipod *Platyscelus ovoides*, a presently undescribed species of lobate ctenophore with vestigial auricles (Undescribed Lobata “No auricles” of Hidaka *et al.* 2021), and cydippid larvae of at least one species of lobate ctenophore (“Cydippid larvae” of Hidaka *et al.* 2021).

Discussion

Santjordia pagesi **gen. et sp. nov.** presents a combination of morphological features not found in any previously-described sennaeostome: subumbrellar rows of tentacles, unbranched radial canals connected by a ring canal away from the margin, and, perhaps the most striking, eight marginal as well as 24 subumbrellar rhopalia. Unfortunately, gonads were not recognized, suggesting it was not quite mature. However, because all subumbrellar tentacles were of the same size and no budding or splitting of radially symmetrical structures was observed, the major morphological features seem unlikely to change before reaching sexual maturity. Based on the general morphological features

of the gastric system and oral arms, according to the existing classification scheme, this new species falls into the family Ulmaridae.

The family Ulmaridae, however, seems to be a catch-all taxon for a wide variety of semaeostome forms that are unable to be grouped into other families. Eight subfamilies are currently recognized within the Ulmaridae (Table 3). Presently, there is no indication as to a character or combination of characters that might group some of these subfamilies into a more reliable classification schema. Some phylogenetic hypotheses have been put forward, mostly based on molecular data (eg. Gómez-Daglio & Dawson 2017), but none of them cover the whole diversity of the family. Without a broad taxonomic covering, any reorganization of the subgroups would be limited and of little use.

TABLE 3. Summary of data and diagnostic characters for distinction of the currently recognized families of “Semaestomeae” medusae. Spp. = number of valid species of the family/subfamily, if the literature mentions undescribed or doubtful species the number was put in brackets and followed by a question mark. Tentacles = presence or absence of tentacles and, if present, how they are organized. Gastrovascular cavity = organization of the cavity, with radial septa, radial canals, ring canal and branching of canals. Gonads = organization of gonads: inverted = contained inside the body; everted = parts of the gonads outside the body. Subgenital ostia = present or absent. Rhopalia = number and position of rhopalia; question mark (?) means that the character is not known for the genus or its state is doubtful. Mostly after: Mayer (1910); Kramp (1961); Russell (1970); Larson (1986); Mianzan & Cornelius (1999); Gershwin & Collins (2002); Matsumoto *et al.* (2003); Raskoff & Matsumoto (2004); Bayha & Dawson (2010); Morandini & Marques (2010); Straehler-Pohl *et al.* (2011); Jarms & Morandini (2019); Collins *et al.* (2022). * signifies character not described in original species description but visible in photograph in Jarms & Morandini (2019).

Family/ Subfamily	Genera	Spp.	Tentacles	Rhopalia	Gastrovascular cavity	Gonads	Subgenital ostia
Pelagiidae Gegenbaur, 1856	<i>Chrysaora</i>	15 (16?)	present, 8, 24, 40, or more, marginal	8, marginal	radial septa, no canals but sometimes with canals on lappets	inverted horse-shoe sometimes protruding	present
	<i>Mawia</i>	1	present, 8, marginal	8 marginal	radial septa, no canals	inverted horse-shoe always protruding	absent
	<i>Pelagia</i>	1 (5?)	present, 8, marginal	8, marginal	radial septa, no canals	inverted horse-shoe sometimes protruding	present
	<i>Sanderia</i>	2	present, 16, marginal	16, marginal	radial septa, no canals	inverted horse-shoe always protruding	present
Cyaneidae Agassiz, 1862	<i>Cyanea</i>	10 (17?)	present, many, subumbrellar groups	8 marginal	radial septa, canals on lappets	everted	absent
	<i>Desmonema</i>	4	present, many, subumbrellar groups	8 marginal	radial septa, canals on lappets	everted	absent
Drymonematidae Haeckel, 1880	<i>Drymonema</i>	3	present, many, subumbrellar zone	8 subumbrellar	radial septa, canals on lappets	everted	absent

...Continued on the next page

TABLE 3. (Continued)

Family/ Subfamily	Genera	Spp.	Tentacles	Rhopaila	Gastrovascular cavity	Gonads	Subgenital ostia
Phacellophoridae Strachler-Pohl <i>et al.</i> , 2011	<i>Phacellophora</i>	1 (3?)	present, many, subumbrellar rows	16 marginal	unbranched and branched canals	everted	absent
Ulmaridae Haeckel, 1880			present or absent		unbranched or branched canals, ring canal on margin	inverted or everted	present or absent
Aureliinae Agassiz, 1862	<i>Aurelia</i>	26 (more?)	present, many, exumbrellar	8 marginal	branched canals	inverted, horse-shoe	present
	<i>Aurosa</i>	1	present, many, exumbrellar	8 marginal	branched canals	inverted, horse-shoe	present
Poraliinae Larson, 1986	<i>Poralia</i>	1 (3?)	present, >50, marginal	16? (12–30) marginal	unbranched canals, ring canal away from margin	inverted, continuous ring	absent
Sthenoniinae Mayer, 1910	<i>Sthenonia</i>	1	present, many, subumbrellar rows	8 marginal	unbranched and branched canals	everted	absent
Ulmarinae Kramp, 1961	<i>Diplulmaris</i>	2	present, 16–48, marginal	16 marginal	unbranched and branched canals	everted	absent
	<i>Discomedusa</i>	2	present, 24–48, marginal	8 marginal	unbranched and branched canals	everted	absent
	<i>Floresca</i>	1	present, 24, marginal	8 marginal	unbranched canals	inverted?, horse-shoe	absent
	<i>Parumbrosa</i>	1	present, 24, marginal	8 marginal	unbranched and branched canals	everted?	absent
	<i>Ulmaris</i>	2	present, 8, marginal	8 marginal	unbranched and branched canals	everted	absent
Deepstariinae Larson, 1986	<i>Deepstaria</i>	2	absent	8–20 marginal	branched canals	on manubrium wall	absent
Stellamedusinae Raskoff & Matsumoto, 2004	<i>Stellamedusa</i>	1	absent	8 marginal	unbranched canals, ring canal away from margin, centripetal canals	inverted, horse-shoe	present
Stygiomedusinae Russell & Rees, 1960	<i>Stygiomedusa</i>	1	absent	20 marginal	branched canals	inverted, horse-shoe	present
Tiburoniinae Matsumoto <i>et al.</i> , 2003	<i>Tiburonia</i>	1	absent	~20–54+ marginal	branched canals	everted*	present
Santjordiinae subfam. nov.	<i>Santjordia</i>	1	present, many, subumbrellar rows	8 marginal + 24 subumbrellar	unbranched canals, ring canal away from margin	?	absent

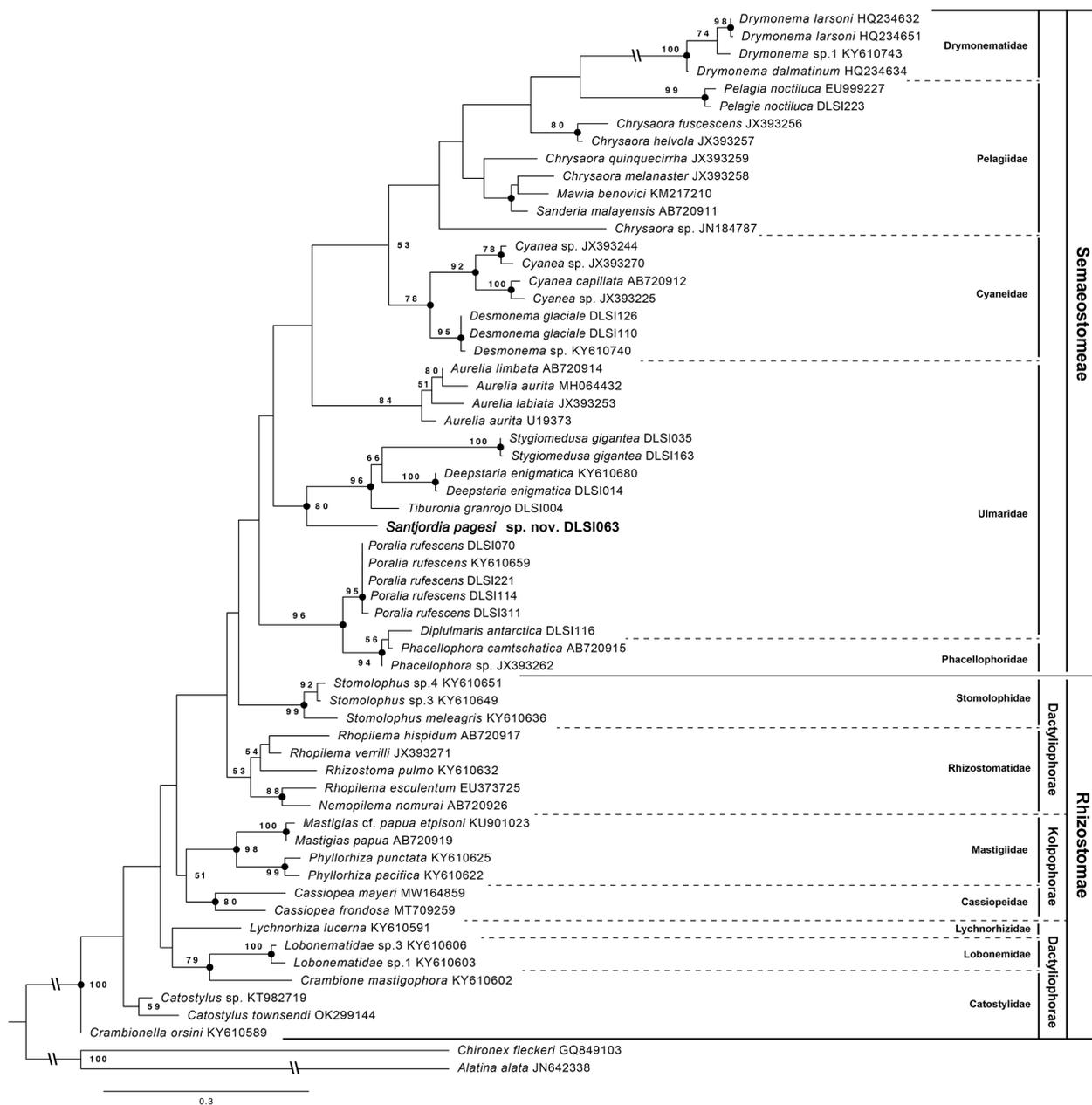


FIGURE 6. Phylogenetic reconstruction based on the 16S-rDNA region for Scyphozoa. Values at nodes indicate ML bootstrap support >50%, and solid circles represent Bayesian probabilities >0.95.

Among the Ulmaridae, tentacles are absent in four of the subfamilies: Stygiomedusinae, Deepstariinae, Tiburoniinae, and Stellamedusinae, thus differing from *Santjordia pagesi* **gen. et sp. nov.** In members of the subfamily Aureliinae, the tentacles arise from the exumbrella above the margin; and in the Poraliinae and Ulmarinae the tentacles arise from clefts in the margin, differing from the subumbrellar position of the tentacles in *Santjordia pagesi* **sp. nov.** Subumbrellar tentacles, such as those found in *Santjordia pagesi* **sp. nov.**, occur in the subfamily Sthenoniinae, but subumbrellar rhopalia, such as found in *Santjordia*, are absent (Table 3). Some other semaeostome families have subumbrellar tentacles (Cyaneidae, Phacellophoridae and Drymonematidae), but in the former two the rhopalia are marginal, and in no species of the genus *Drymonema*, currently the only genus in the Drymonematidae (Bayha & Dawson 2010), do additional rhopalia, rows of tentacles, or radial or ring canals occur.

In the analysis of 16S gene sequences, the *Santjordia pagesi* **gen. et sp. nov.** specimen clustered with a subgroup of subfamilies morphologically attributable to the family Ulmaridae, which appears to be a polyphyletic grouping (Fig. 6). This subgroup contains the subfamilies Stygiomedusinae Russell & Rees, 1960, Deepstariinae Larson,

1986 and Tiburoniinae Matsumoto *et al.*, 2003, which are united with strong support in both the ML and Bayesian analyses (Fig. 6). No genetic information is available for the subfamily Stellamedusinae Raskoff & Matsumoto, 2004, another taxon lacking marginal or subumbrellar tentacles. The present study groups *Santjordia pagesi* **gen. et sp. nov.** with this subgroup with a Bayesian probability of 97%. The obvious morphological differences and the lack of support for this clade's position within any other scyphozoan clade is probably related to poor taxon sampling in combination with a relatively rapidly evolving genetic marker. Without a more detailed, multi-marker genetic analysis with new material, a taxonomic revision of the Ulmaridae and/or the erection of a new family for *Santjordia pagesi* **gen. et sp. nov.** would be premature. Furthermore, as the purpose of a taxonomic classification scheme is to facilitate information retrieval and the usefulness of a classification as a communication system stands in direct relation to its stability (Mayr & Ashlock 1991), we choose to be conservative in our classification at the present time until the full diversity of this group has been more properly ascertained and the possible effect of artefacts due to taxon-sampling is resolved. Particularly with respect to DNA analyses, the erection of new higher taxa notwithstanding imperfect taxon sampling seems inadvisable. To illustrate this, the present analysis grouped *Diplulmaris antarctica* (Ulmaridae: Ulmarinae), the type of the genus, with the recently erected family Phacellophoridae (Straehler-Pohl *et al.* 2011) with a Bayesian probability of 100% (Fig. 6). This clade was in turn sister to, and within, a clade also containing *Poralia rufescens* Vanhöffen, 1902 (Ulmaridae: Poraliinae) with a Bayesian probability of 100% (Fig. 6). Contrastingly, specimens morphologically attributable to *P. rufescens*, with the exception of a 10.8-mm diameter animal with 30 tentacles (GenBank ID ON391162) for which this is the first published report of a juvenile specimen and a morphological comparison was therefore impossible, clustered together with a Bayesian probability of only 95% (Fig. 6, Table 1). Rather than erect a new family at this time, we conservatively propose the erection of a new subfamily, Santjordiinae, within the Ulmaridae, based on the current morphologically-based diagnoses of families, to include this novel medusa. It is expected that further surveys in the deep ocean will continue to discover novel scyphomedusan taxa and redefine our understandings of the evolution of this group.

The present species has so far only been found inside the Sumisu Caldera and has not been observed anywhere else during over a hundred hours of *in situ* deep-sea exploration in other waters around Japan (*e.g.*, Lindsay & Hunt 2005; Lindsay *et al.* 2015; Hidaka *et al.* 2021) or during midwater dives in other areas around the world (Schmidt Ocean Institute 2022, NOAA Archives 2022).

Acknowledgements

We are grateful to the reviewers for critical and constructive comments on the manuscript and nomenclature employed. Appreciation is due to Allen Collins of the National Museum of Natural History, Smithsonian Institution, and to Nanae Fukumoto, then at Kitasato University, for sequencing some of the material used in the DNA analyses. Thanks are due to Dr. Carina Östman for confirmation of nematocyst types. We also thank Dr. Hiroyuki Yamamoto of the Environmental Impact Assessment Research Group, within the Research and Development Center for Submarine Resources, JAMSTEC, and Satoshi Mitarai of OIST, for their support. We would like to express our appreciation to the captain and crew of the R/V *Kaiyo*, as well as to the operations team and commander of the ROV *Hyper-Dolphin*. The 2008 CEAMARC Cruise of the TRV *Umitaka Maru* to eastern Antarctica (PIs Takashi Ishimaru & Grahame Hosie) provided material for the analyses with DJL's travel being funded by the Census of Marine Zooplankton (CMarZ) within the Census of Marine Life (CoML). CMarZ also funded DJL's travel for the R/V *Ronald H. Brown* survey in the Caribbean. We appreciate the opportunity given DJL for a 5-month sabbatical at CSIC, Barcelona, in 2005 by the Japan Society for the Promotion of Science. This work was partially funded by Japan Society for the Promotion of Science (JSPS) KAKENHI grant numbers 24248032, 26304030 and 23405031, JST grant CREST, the Cross-ministerial Strategic Innovation Promotion Program (SIP) for the Development of New-generation Research Protocols for Submarine Resources, MEXT Grant-in-Aid for Scientific Research on Innovative Areas TAIGA (20109003); grants CNPq 307832/2022-8, 2010/50174-7, 2011/50242-5 and 2013/05510-4 São Paulo Research Foundation (FAPESP). This study is a contribution to the International Network for Scientific Investigations of Deep-Sea Ecosystems (INDEEP), the Deep Ocean Stewardship Initiative (DOSI), and NP-BioMar, USP.

Author Contributions

DJL did the field work and conceptualized the project. DJL and MMG performed morphological measurements. MMG performed some of the DNA lab work and drew the illustrations under the supervision of DJL. JM performed the data analysis for genetic data. ACM identified nematocysts and provided morphological information on other ulmarids. All authors contributed to the species description and the writing and reviewing of the manuscript.

References

- Appeltans, W., Ah Yong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Błażewicz-Paszkwowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandão, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.Y., Chan, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J.F., Dawson, M.N., De Clerck, O., De Cock, W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hoeksema, B.W., Hopcroft, R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P., Meland, K.L., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Rosenberg, G., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, A., Turon, X., Tyler, S., Uetz, P., van der Land, J., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Vanhoorne, B., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G., Wilson, S.P., Hernandez, F., Mees, J. & Costello, M.J. (2012) The magnitude of global marine species diversity. *Current Biology*, 22, 1–14.
<https://doi.org/10.1016/j.cub.2012.09.036>
- Avian, M., Ramsak, A., Tirelli, V., D'Ambra, I. & Malej, A. (2016) Redescription of *Pelagia benovici* into a new jellyfish genus, *Mawia*, **gen. nov.**, and its phylogenetic position within Pelagiidae (Cnidaria: Scyphozoa: Semaestomeae). *Invertebrate Systematics*, 30 (6), 523–546.
<https://doi.org/10.1071/IS16010>
- Bayha, K.M. & Dawson, M.N. (2010) New family of allomorphic jellyfishes, Drymonematidae (Scyphozoa, Discomedusae), emphasizes evolution in the functional morphology and trophic ecology of gelatinous zooplankton. *Biological Bulletin*, 219, 249–267.
<https://doi.org/10.1086/BBLv219n3p249>
- Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17 (4), 540–552.
<https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Collins, A.G., Jarms, G. & Morandini, A.C. (2022) World List of Scyphozoa. Semaestomeae. Accessed through: World Register of Marine Species. Available from: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=135225> (accessed 15 April 2022)
- Collins, A.G., Bentlage, B., Lindner, A., Lindsay, D., Haddock, S.H.D., Jarms, G., Norenburg, J.L., Jankowski, T. & Cartwright, P. (2008) Phylogenetics of Trachylina (Cnidaria: Hydrozoa) with new insights on the evolution of some problematical taxa. *Journal of the Marine Biological Association of the United Kingdom*, 88, 1673–1685.
<https://doi.org/10.1017/S0025315408001732>
- Cornelius, P.F.S. (1997a) Class Scyphozoa—jellyfish. In: Richmond, M.D. (Ed.), *A guide to the seashores of eastern Africa and the western Indian Ocean islands*. SIDA/Department for Research Cooperation, SAREC, Stockholm, pp. 122–125.
- Cornelius, P.F.S. (1997b) Keys to the genera of cubomedusae and scyphomedusae (Cnidaria). In: den Hartog, J.C. (Ed.), *Proceedings of the 6th International Conference on Coelenterate Biology. 1995*. Nationaal Natuurhistorisch Museum, Leiden, pp. 109–122.
- Cunningham, C.W. & Buss, L.W. (1993) Molecular Evidence for Multiple Episodes of Paedomorphosis in the Family Hydractiniidae. *Biochemical Systematics and Ecology*, 21 (1), 57–69.
[https://doi.org/10.1016/0305-1978\(93\)90009-G](https://doi.org/10.1016/0305-1978(93)90009-G)
- Daly, M., Brugler, M.R., Cartwright, P., Collins, A.G., Dawson, M.N., Fautin, D.G., France, S.C., McFadden, C.S., Opresko, D.M., Rodriguez, E., Romano, S.L. & Stake, J.L. (2007) The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*, 1668, 127–182.
<https://doi.org/10.11646/zootaxa.1668.1.11>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) JModelTest 2: More Models, New Heuristics and Parallel Computing. *Nature Methods*, 9 (8), 772.
<https://doi.org/10.1038/nmeth.2109>
- Dawson, M.N. (2003) Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria:

- Scyphozoa). *Marine Biology*, 143, 369–379.
<https://doi.org/10.1007/s00227-003-1070-3>
- Dawson, M.N. (2005) Five new subspecies of *Mastigias* (Scyphozoa: Rhizostomeae: Mastigiidae) from marine lakes, Palau, Micronesia. *Journal of the Marine Biological Association of the United Kingdom*, 85, 679–694.
<https://doi.org/10.1017/S0025315405011604>
- Dawson, M.N. & Jacobs, D.A. (2001) Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). *Biological Bulletin*, 200, 92–96.
<https://doi.org/10.2307/1543089>
- Gershwin, L. & Collins, A.G. (2002) A preliminary phylogeny of Pelagiidae (Cnidaria: Scyphozoa), with new observations of *Chrysaora colorata* comb. nov. *Journal of Natural History*, 36, 127–148.
<https://doi.org/10.1080/00222930010003819>
- Gershwin, L. & Zeidler, W. (2008) Two new jellyfishes (Cnidaria: Scyphozoa) from tropical Australian waters. *Zootaxa*, 1764 (1), 41–52.
<https://doi.org/10.11646/zootaxa.1764.1.4>
- Gómez-Daglio, L. & Dawson, M.N. (2017) Species richness of jellyfishes (Scyphozoa: Discomedusae) in the Tropical Eastern Pacific: missed taxa, molecules, and morphology match in a biodiversity hotspot. *Invertebrate Systematics*, 31 (5), 635–663.
<https://doi.org/10.1071/IS16055>
- Hidaka, M., Nishikawa, J. & Lindsay, D.J. (2021) Gelatinous zooplankton community around a hydrothermally active deep-sea caldera: results from ROV video records. *Plankton and Benthos Research*, 16 (1), 40–58.
<https://doi.org/10.3800/pbr.16.40>
- Jarms, G. & Morandini, A.C. (Eds.) (2019) *World Atlas of Jellyfish, 11 January 2019*. Dölling und Galitz Verlag, Hamburg, 816 pp. [ISBN: 3862180824]
- Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*, 30 (4), 772–780.
<https://doi.org/10.1093/molbev/mst010>
- Kitamura, M., Miyake, H. & Lindsay, D.J. (2008) Cnidaria. In: Fujikura, K., Okutani, T. & Maruyama, T. (Eds.), *Deep-sea life—Biological observations using research submersibles*. Tokai University Press, Kanagawa, 295–320.
- Kramp, P.L. (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom*, 40, 7–469.
<https://doi.org/10.1017/S0025315400007347>
- Larson, R.J. (1986) Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaestomeae) of the Southern Ocean. *Antarctic Research Series*, 41, 59–165.
<https://doi.org/10.1029/AR041p0059>
- Lindsay, D.J. (2003) Bioluminescence in the mesopelagic realm. *Kaiyo Monthly, Special Edition*, 35 (9), 606–612.
- Lindsay, D.J., Furushima, Y., Miyake, H., Kitamura, M. & Hunt, J.C. (2004) The scyphomedusan fauna of the Japan Trench: preliminary results from a remotely-operated vehicle. *Hydrobiologia*, 530/531, 537–547.
<https://doi.org/10.1007/s10750-004-2645-9>
- Lindsay, D.J. & Hunt, J.C. (2005) Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and North-western Pacific. *Journal of the Marine Biological Association of the United Kingdom*, 85 (3), 503–517.
<https://doi.org/10.1017/S0025315405011434>
- Lindsay, D.J., Pagès, F., Corbera, J., Miyake, H., Hunt, J.C., Ichikawa, T., Segawa, K. & Yoshida, H. (2008) The anthomedusan fauna of the Japan Trench: preliminary results from in situ surveys with manned and unmanned vehicles. *Journal of the Marine Biological Association of the United Kingdom*, 88 (8), 1519–1539.
<https://doi.org/10.1017/S0025315408002051>
- Lindsay, D.J., Umetsu, M., Grossmann, M.M., Miyake, H. & Yamamoto, H. (2015) Chapter 51. The gelatinous macroplankton community at the Hatoma Knoll hydrothermal vent. In: Ishibashi, J., Okino, K. & Sunamura, M. (Eds.), *Subseafloor Biosphere Linked to Global Hydrothermal Systems; TAIGA Concept*. Springer, Tokyo, pp. 639–666.
https://doi.org/10.1007/978-4-431-54865-2_51
- Lindsay, D.J. (2022a) In situ ROV video of *Santjordia pagesi* holotype specimen HD84GS1 (DLSI063). *Dataset on Zenodo*. [Zenodo version is H264 transcoded]
<https://doi.org/10.5281/zenodo.6426355>
- Lindsay, D.J. (2022b) In situ ROV video of *Santjordia pagesi* second individual. *Dataset on Zenodo*. [Zenodo version is H264 transcoded]
<https://doi.org/10.5281/zenodo.6480798>
- Lindsay, D.J. (2022c) Photographs in gate sampler of *Santjordia pagesi* holotype specimen HD84GS1 (DLSI063). *Dataset on Zenodo*.
<https://doi.org/10.5281/zenodo.6420570>
- Lindsay, D.J. (2022d) Photographs under microscope of *Santjordia pagesi* holotype specimen HD84GS1 (DLSI063) tentacle squashes. *Dataset on Zenodo*.

- <https://doi.org/10.5281/zenodo.6424652>
- Lindsay, D.J. (2022e) In situ ROV video of *Deepstaria enigmatica* specimen HD98SS1 (DLSI014). *Dataset on Zenodo*. [Zenodo version is H264 transcoded]
<https://doi.org/10.5281/zenodo.6475523>
- Lindsay, D.J. (2022f) Laboratory video of *Deepstaria enigmatica* specimen HD98SS1 (DLSI014). *Dataset on Zenodo*. [Zenodo version is H264 transcoded]
<https://doi.org/10.5281/zenodo.6480763>
- Lindsay, D.J. (2022g) Photographs under microscope of *Desmonema glaciale* specimen UM12_RMT200_Dg (DLSI110). *Dataset on Zenodo*.
<https://doi.org/10.5281/zenodo.6471770>
- Lindsay, D.J. (2022h) Photograph of *Poralia rufescens* specimen UM17_RMT-D-8-1_Pr (DLSI114). *Dataset on Zenodo*.
<https://doi.org/10.5281/zenodo.6471820>
- Lindsay, D.J. (2022i) Video under microscope of *Poralia rufescens* specimen 2K1201SS4b_Pr_juv (DLSI311). *Dataset on Zenodo*.
<https://doi.org/10.5281/zenodo.6472194>
- Lindsay, D.J. (2022j) Photographs of *Stygiomedusa gigantea* specimen UM14_IYGPT500_Sg (DLSI163). *Dataset on Zenodo*.
<https://doi.org/10.5281/zenodo.6471790>
- Lindsay, D.J. (2022k) *In situ ROV video of Tiburonia granrojo specimen HD99SS1*. *Dataset on Zenodo*. [Zenodo version is H264 transcoded]
<https://doi.org/10.5281/zenodo.6476641>
- Lucas, C.H., Pitt, K.A., Purcell, J.E., Lebrato, M. & Condon, R.H. (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. *Ecology*, 92 (8), 1704.
<https://doi.org/10.1890/11-0302.1>
- Matsumoto, G.I., Raskoff, K.A. & Lindsay, D.J. (2003) *Tiburonia granrojo* n. sp., a mesopelagic scyphomedusa from the Pacific Ocean representing the type of a new subfamily (class Scyphozoa: order Semaestomeae: family Ulmaridae: subfamily Tiburoniinae **subfam. nov.**). *Marine Biology*, 143, 73–77.
<https://doi.org/10.1007/s00227-003-1047-2>
- Mayer, A.G. (1910) n.k. In: *The medusae of the world. Vol.III. The Scyphomedusae. Carnegie Institution of Washington Publication 109*. Carnegie Institution of Washington, Washington, D.C., pp. 499–735.
- Mayr, E. & Ashlock, P.D. (1991) Principles of systematic zoology. McGraw Hill, New York, 475 pp.
- Mianzan, H.W. & Cornelius, P.F.S. (1999) Cubomedusae and Scyphomedusae. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 513–559.
- Morandini, A.C. & Marques, A.C. (2010) Revision of the genus *Chrysaora* Péron & Lesueur, 1810 (Cnidaria: Scyphozoa). *Zootaxa*, 2464 (1), 1–97.
<https://doi.org/10.11646/zootaxa.2464.1.1>
- Nishikawa, J., Ohtsuka, S., Mulyadi, Mujiono, N., Lindsay, D.J., Miyamoto, H. & Nishida, S. (2014) A new species of the commercially harvested jellyfish *Crambionella* (Scyphozoa) from central Java, Indonesia with remarks on the fisheries. *Journal of the Marine Biological Association of the United Kingdom*, 95 (3), 471–481.
<https://doi.org/10.1017/S002531541400157X>
- NOAA Archives (2022) *Video data collected during midwater dive surveys on NOAA Ship Okeanos Explorer. Subset of multiple dives in Pacific and Atlantic Oceans where D.J. Lindsay was a registered participant*. NOAA National Centers for Environmental Information, EX FTP Server. (accessed 11 April 2022) [some videos publicly available on <https://www.youtube.com/user/oceanexplorergov>]
- Piraino, S., Aglieri, G., Martell, L., Mazzoldi, C., Melli, V., Milisenda, G., Scorrano, S. & Boero, F. (2014) *Pelagia benovici* **sp. nov.** (Cnidaria, Scyphozoa): a new jellyfish in the Mediterranean Sea. *Zootaxa*, 3794 (3), 455–468.
<https://doi.org/10.11646/zootaxa.3794.3.7>
- Raskoff, K.A. & Matsumoto, G.I. (2004) *Stellamedusa ventana*, a new mesopelagic scyphomedusae from Monterey Bay, CA representing a new subfamily, the Stellamedusinae. *Journal of the Marine Biological Association of the United Kingdom*, 84, 37–42.
<https://doi.org/10.1017/S0025315404008884h>
- Ronquist, F.R. & Huelsenbeck, J.P. (2003) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 19 (12), 1572–1574.
<https://doi.org/10.1093/bioinformatics/btg180>
- Russell, F.S. (1970) *The medusae of the British Isles II. Pelagic Scyphozoa with a supplement to the first volume on hydromedusae*. Cambridge University Press, London, 284 pp.
- Schmidt Ocean Institute (2022) R/V Falkor and ROV SuBastian Video Dataset on YouTube. Available from: <https://www.youtube.com/c/SchmidtOcean> (accessed 11 April 2022)
- Scorrano, S., Aglieri, G., Boero, F., Dawson, M.N. & Piraino, S. (2017) Unmasking *Aurelia* species in the Mediterranean Sea: An integrative morphometric and molecular approach. *Zoological Journal of the Linnean Society*, 180, 243–267.
<https://doi.org/10.1111/zoj.12494>
- Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.

<https://doi.org/10.1111/zoj.12494>

Straehler-Pohl, I., Widmer, C.L. & Morandini, A.C. (2011) Characterizations of juvenile stages of some semaeostome Scyphozoa (Cnidaria), with recognition of a new family (Phacellophoridae). *Zootaxa*, 2741 (1), 1–37.

<https://doi.org/10.11646/zootaxa.2741.1.1>

Tani, K., Fiske, R.S., Tamura, Y., Kido, Y., Naka, J., Shukuno, H. & Takeuchi, R. (2008) Sumisu volcano, Izu-Bonin arc, Japan: site of a silicic caldera-forming eruption from a small open-ocean island. *Bulletin of Volcanology*, 70, 547–562.

<https://doi.org/10.1007/s00445-007-0153-2>