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ORIGINAL PAPER

Redescription and neotype designation of *Aglauropsis kawari* Moreira & Yamashita, (Cnidaria: Hydrozoa, Limnomedusae) based on an integrative taxonomy approach

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Abstract

Aglauropsis kawari Moreira & Yamashita, 1972 (Cnidaria: Hydrozoa: Limnomedusae: Olindiidae) was originally described solely on the basis of formalin-preserved material, leading to morphological inconsistencies and not providing crucial details on juvenile individuals and the cnidome. Subsequent records similarly lacked comprehensive data. The present study addresses these gaps by providing a detailed redescription of *A. kawari* based on newly collected, live specimens from the São Sebastião Channel, São Paulo State, Brazil, and preserved material from the type locality (Rio Grande do Sul State). We provide high-quality photographs of living individuals, morphometric analyses across different maturity stages (young, subadult, mature), and a comprehensive cnidome description. Given the loss of the original type material and inaccuracies in the original description, a neotype is designated herein for *A. kawari*. A molecular characterization, based on 16S and 28S ribosomal DNA markers, provides insights into its phylogenetic placement within the family Olindiidae Haeckel, 1879. The 16S tree groups *A. kawari* with *Vallentinia gabriellae* Vannucci Mendes, 1948, whereas the 28S tree shows a stronger relationship with *Aglauropsis aeora* Mills, Rees & Hand, 1976. The reconstruction based on the concatenated dataset (16S+28S) provided a more robust phylogenetic tree, resolving these incongruences. The integrated approach clarifies the species identity, establishes reliable diagnostic characters, and enhances its taxonomic understanding, contributing to a broader knowledge of the Limnomedusae diversity in the southwestern Atlantic.

Keywords Medusa · Neotype · Olindiidae · Phylogenetics · Taxonomy

Introduction

The Limnomedusae Kramp, 1938, a small group within Trachylinae Haeckel, 1879, currently includes 40 valid species (Schuchert et al. 2025). This clade was first established as an order by Kramp (1938), to accommodate medusae from various genera whose systematic placement had always been considered problematic (Russell 1953). Historically, Bouillon and Boero (2000) recognized two families within Limnomedusae: the monotypic Armorhydridae Swedmark & Teissier, 1958 and Olindiidae Haeckel, 1879 (then with 31 valid species). However, Marques and Collins (2004), in their cladistic analysis where Limnomedusae was treated as a single terminal, highlighted potential polyphyly due to the lack of autapomorphies and previous alternative assignments of some Limnomedusae groups to other clades, such as Trachymedusae or Anthoathecata. They identified only one synapomorphy for the group, i.e. the presence of a continuous ring of cnidae on the umbrellar margin of the medusae.

More recently, phylogenetic inferences based on molecular data, with species as terminals, have significantly advanced our understanding of Trachylinae evolution (Collins et al. 2008; Bentlage et al. 2018; Osadchenko and Kraus 2018). These studies have provided a revised framework: (i) Limnomedusae is now recognized as a sister group to a clade comprising Trachymedusae and Narcomedusae within the subclass Trachylinae; (ii)

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Limnomedusae now comprises five recognized families: Geryoniidae Eschscholtz, 1829 (2 genera, 2 species; both species with molecular data supporting monophyly), Monobrachiidae Mereschkowsky, 1877 (1 genus, 3 species; with molecular data available for *Monobrachium parasiticum* Mereschkowsky, 1877), Microhydrulidae Bouillon & Deroux, 1967 (2 genera, 2 species; no molecular data currently available), Olindiidae (15 genera, 48 species; most genera with molecular data, though the family itself is not monophyletic, see details in Bentlage et al. 2018), and Armorhydridae (1 genera and 1 species; no molecular data currently available); (iii) while most Limnomedusae species exhibit full metagenetic life cycle (succession between sessile polyp and free-swimming medusa), this group presents all three possibilities: 1. metagenetic cycle; 2. holoplanktonic cycle, which lack a sessile polyp stage (e.g. Geryoniidae); and 3. polyp-only species, where the medusa stage is absent, as seen in the epizoic *M. parasiticum*. An updated diagnosis was proposed by Bentlage et al. (2018), as an "emended diagnosis for Limnomedusae: Hydroid, if present, small, simple, mostly solitary, some forming colonies; sessile; with or without tentacles; without theca but having a mucoprotein periderm, cysts and stolons can be covered by perisarc. Medusa mostly with 4 complete radial canals, 6 also possible, often with incomplete centripetal canals not reaching manubrium; with or without marginal nematocyst ring; gonads along radial canals or exceptionally on manubrium (genera *Armorhydra* and *Limnocnida*); marginal tentacles peripheral, hollow, or solid and hollow (Geryoniidae), without true basal bulb; marginal sense organs as internal enclosed statocysts of endo-ectodermal origin, embedded in the mesoglea near ring canal or in the velum; no ocelli; exceptionally reduced medusoids (genus *Monobrachium*). Predominantly found in nearshore waters."

The genus *Aglauropsis* Müller, 1865 (containing six valid species and one *taxon inquirendum*) is morphologically characterized by the presence of holotrichous nematocysts (Bouillon 1985), the absence of centripetal canals, solitary marginal tentacles lacking adhesive pads, and four radial canals where gonads develop. The genus is currently assigned to the family Olindiidae. Phylogenetic analysis revealed that the family is not monophyletic. Several of its genera group into different clades within Limnomedusae, suggesting that the family, as traditionally defined, is polyphyletic (Bentlage et al. 2018).

Marine waters of South America host a diverse medusozoan fauna. The census of Oliveira et al. (2016) lists 780 species of Medusozoa for the region, including 748 species of Hydrozoa, of which 11 belong to the order Limnomedusae. Five of these are recorded from the Brazilian coast, although one of them (*M. parasiticum*) lacks a medusa stage in its life cycle (Migotto et al. 2002; Oliveira et al. 2016). Within this context, *Aglauropsis kawari* Moreira & Yamashita, 1972, is of a particular taxonomical and ecological interest. Since its original description, occurrences of this limnomedusa have been reported in low abundances during mesozooplankton surveys conducted in coastal areas of the southwestern Atlantic (Moreira and Yamashita 1972; Zamponi 1992; Zamponi and Genzano 1994; Genzano et al. 2008; Nogueira Jr. et al. 2014; Nascimento et al. 2019; Cruz and Siquier 2019; Dutto et al. 2019; Teixeira-Amaral et al. 2021).

The original description of *A. kawari* was solely based on formalin-preserved materials, a method known to induce morphological artefacts, leading to taxonomic inconsistencies (e.g. Schuchert and Collins 2021; Martinez et al. 2013). Their account lacked details on juvenile individuals and a complete characterization of the cnidome. Subsequent records of *A. kawari* (Genzano et al. 2008; Nogueira et al. 2014; Nascimento et al. 2019; Teixeira-Amaral et al. 2021), while confirming and extending its known distribution (e.g. to São Paulo State, including the material studied herein), similarly lacked comprehensive morphological data and the cnidome characterization. The absence of a designated type-specimen by Moreira and Yamashita (1972), coupled with the loss of their original material, further hinders a reliable taxonomic verification of *A. kawari*.

In this study, we address these critical gaps by providing a comprehensive redescription of *A. kawari* based on newly collected specimens. Our work includes high-resolution photographs of living individuals, morphometric analyses across different maturity stages, a molecular characterization, and a documentation of its cnidome. The integrative approach aims to correct preservation-induced artifacts, establish reliable diagnostic morphological characters, and enhance the overall understanding of the species identity and its taxonomic placement, for which we also designate a neotype. Finally, we briefly discuss general trends in the evolution of the genus *Aglauropsis*.

Material and methods

Aglauropsis kawari medusae were collected during various hydromedusae surveys conducted in the São Sebastião Channel, São Paulo State, Brazil, from January 1999 to May 2000, and from January 2004 to July 2005, with additional collections in 2015 and 2019. Sampling employed standard plankton nets of 300 and 500 µm mesh, selected to retain small medusae while minimizing mechanical damage to gelatinous taxa. Vertical hauls were performed from near-bottom to surface using a metered nylon cable; a 1.5 kg weight

was attached posteriorly to maintain the net in a vertical position and to avoid bottom contact and sediment entrainment. Retrieval was manual, continuous, and slow to reduce turbulence and plankton compaction in the cod end. Horizontal hauls were conducted 10–30 cm below the surface from a low-speed motorboat; the two nets were towed simultaneously on opposite sides of the vessel. Tow duration was deliberately short and empirically defined to reduce clogging and physical damage: 2 min for the 300 µm net and 4 min for the 500 µm net. Immediately after collection, plankton was transferred to insulated containers completely filled with seawater to reduce internal water movement and consequent specimen damage; samples were transported to the laboratory within ~ 20–40 min for immediate sorting. At each station, water-column temperature and salinity were characterized using a Nansen bottle equipped with two reversing thermometers, collecting four discrete water samples (near-bottom, at 10 m intervals, and at 5 m below the surface). Salinity aliquots were measured with a temperature-compensated refractometer (Reichert, model 10,419). Because the nets were not closing devices, the exact depth stratum of capture for each individual could not be determined; thus, abiotic values are reported for the sampled water column associated with hauls in which the species occurred. In these hauls, *A. kawari* was recorded across a temperature range of 17.65–27.50 °C and salinity of 34–36. Additional preserved material from Patos Lagoon estuary, Rio Grande do Sul State (32°9.76'S, 52°6.24'W), the species type locality, was collected in the frame of the Long-term Ecological Research Program (PELD – Site 8), through sub-surface (3–5 m) horizontal tows (2–5 min) using a 30 cm-diameter plankton net with a 200 µm mesh size.

Medusae were maintained alive in plastic or glass bowls containing filtered seawater for up to 14 days. Specimens were inspected daily under a stereomicroscope, after which the water in the culture dishes was completely replaced. Planktonic organisms and *Artemia* sp. nauplii were offered as food; despite daily feeding attempts, no ingestion was observed.

Photographs of living medusae were acquired from specimens kept in aquaria and under light microscopy, following a 12 to 24-h cultivation period to allow recovery from potential collection damage. This approach directly addresses the challenges often faced with preserved gelatinous organisms, aligning with the call by Schuchert and Collins (2021) for superior photographic documentation to enhance species characterization. The sex of the examined specimens was assessed based on gonad morphology under stereomicroscopy. Although several individuals possessed well-developed gonads and could be of the male phenotype, no further high-magnification microscopy or histological analyses were conducted to confirm the presence of spermatogenic follicles. Since no oocytes (characterized as distinct, large spherical cells) were observed to definitively identify females, all material, including the neotype, is reported as sex indeterminate to avoid taxonomic over-interpretation.

Nematocyst types and distribution were documented using a light microscope equipped with interference-contrast optics; nematocyst measurements were done in vivo. Nematocyst nomenclature follows Mariscal (1974) and Östman (2000). Types were identified based on the morphological analysis of the capsule shape, the presence of a shaft, and the characteristics of the tubule (e.g., presence and distribution of spines).

All morphometric data were obtained from live specimens under a stereomicroscope equipped with an ocular micrometer, immediately after collection or, when specimens were damaged or contracted, after several hours or on the following day. Voucher specimens were anesthetized in a 1:1 mixture of seawater and 7.5% $MgCl_2$ solution and fixed in 4% formaldehyde solution in seawater. Specimens intended for molecular characterization were preserved in 99% ethanol immediately following collection. DNA extraction was destructive; consequently, extracted individuals were not retained as morphological vouchers. Sampling was conducted at two distinct regions along the Brazilian coast: (1) São Paulo (23°50.13'S, 45°25.15'W), where five specimens ($n = 5$) were obtained on 10 October 2022 at 22.5 °C and salinity of 33; and (2) the type locality in Rio Grande do Sul (32°9.76'S, 52°6.24'W), where twenty specimens ($n = 20$) were collected on 24 August 2017 (abiotic parameters not recorded). All collections followed the standardized sampling protocols detailed above for each respective site.

Specimens examined herein are deposited in the following institutions: Centro de Biodiversidade Subtropical of the Universidade Federal do Rio Grande (CBS—FURG), and the Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil.

Genetic analysis

Total DNA extraction was performed in one specimen from each locality using the Bio-Rad® INSTAGENE kit (Nishiguchi et al. 2002), and quality control was performed with a Thermo® NanoDrop 2000c spectrophotometer (230/260/280 ratios). Polymerase Chain Reaction (PCR) was conducted for two ribosomal molecular markers: partial mitochondrial 16S (annealing temperature: 55 °C) and partial nuclear 28S (annealing temperature: 55 °C) rRNA genes (Littlewood et al. 1994; Tkach et al. 1999; Wade and Mordan 2000; Williams and Ozawa 2006; Lawley et al. 2016). Detailed

Table 1 Primers used for DNA amplification and sequencing

Marker	Primer Name	Sequence (5'–3')	Reference
16S	medrnlF	GACTGTTTACCAAAGACATAGC	Lawley et al. (2016)
	medrnlR	AAGATAGAAACCTTCCTGTC	Lawley et al. (2016)
28S	LSU5	TAGGTCGACCCGCTGAAYTTAAGCA	Littlewood et al. (1994)
	LSU330F	CAAGTACCGTGAGGGAAAGTTG	Williams and Ozawa (2006)
	LSU1500R	GCTATCCTGAGGGAAACTTCG	Tkach et al. 1999

information regarding the primers used, including their sequences and original references, is summarized in Table 1.

The PCR program was set up with a traditional protocol: initial denaturation 95 °C (5 min); 35 cycles of denaturation (95 °C × 40 s), annealing (55 °C × 50 s), and extension (72 °C × 60 s); final, single 72ºC extension for 7 min. Successful PCR products were verified with a 1% agarose gel and purified using the Agencourt AMPure® kit. Big Dye reaction was carried out with the same PCR primers using the ABI Big Dye V3.1® kit. Finally, sequencing was performed with a Hitachi® ABI PRISM3100 genetic analyzer (IB-USP facility). Individual forward and reverse chromatograms were assembled in Geneious® v9.14 (Drummond et al. 2011), and sequences were checked for contamination using BLAST, and finally submitted to GenBank (Altschul et al. 1990) (see GenBank codes and main data in Supplementary Table S1). Sequences from both localities, São Paulo and the Rio Grande do Sul State, were similar for the analyzed molecular markers. Genetic distances were calculated (uncorrected values in Geneious® 9.14) and phylogenetic trees were generated for the family Olindiidae based on the aforementioned ribosomal molecular markers, combining our new sequences and the available data from GenBank. Phylogenies were inferred for each gene individually, and a combined 16S + 28S dataset was also analyzed. Each marker was independently aligned using the MAFFT program as part of Geneious® 9.14, and low-quality and non-overlapping ends were trimmed. Alignments were then combined in SequenceMatrix (Vaidya et al. 2011). Phylogenetic analysis was performed with IQ-TREE v2.4 using the Maximum Likelihood (ML) criterion, with the evolutionary model and optimal partitioning determined automatically (Nguyen et al. 2015; Minh et al. 2020). The search for the optimal ML tree included four support methods: non-parametric Bootstrap and SH-aLRT (both with 1000 pseudoreplicates), and parametric aLRT and aBayes (both with 1000 replicates). High support branches were recognized when at least three of four applied methods presented high values as follows: non-parametric bootstrap (BS) 75%, approximate BAYES (aBAYES) 0.95; approximate likelihood ratio test (aLRT) 0.9; SH-like (SH-aLRT) 0.85 (Anisimova et al. 2011).

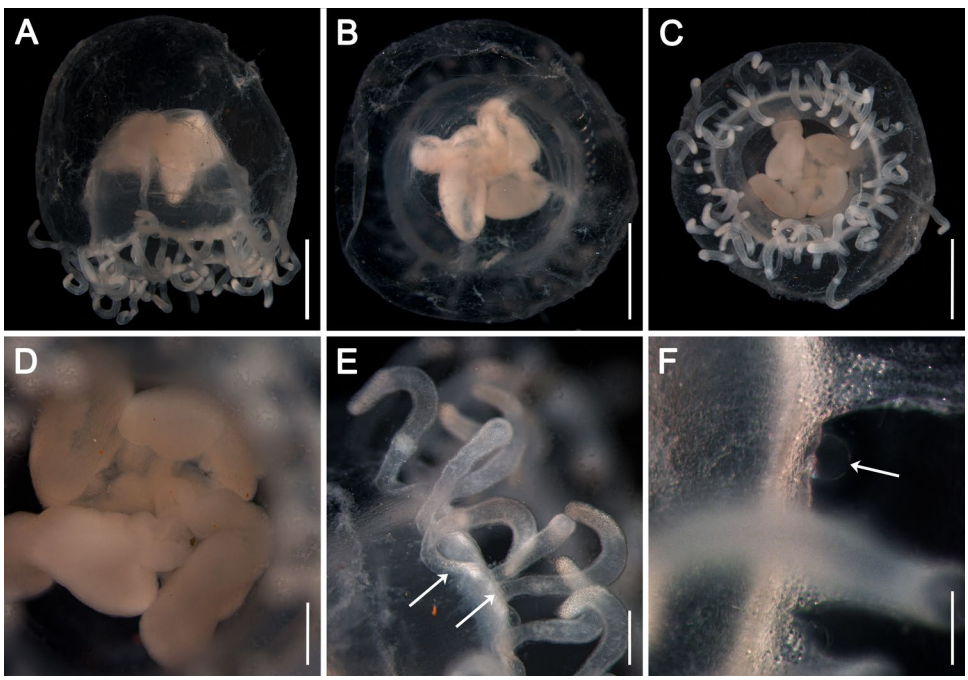

Fig. 1 *Aglauropsis kawari* Moreira & Yamashita, 1972, neotype (CBS ZOO 000185). **A** Lateral view; **B** Apical view, showing the arrangement of the gonads; **C** Oral view detailing the margin of umbrella, velum and tentacles; **D** Oral view showing the pouch-like gonads obscuring the manubrium; **E** Detail of tentacles showing insertion types (white arrows indicate distinct tentacle insertion positions) and elongated terminal swellings packed with nematocysts; **F** Marginal view showing statocyst (white arrow). Scale bars: 1 mm (**A**–**C**), 0.25 mm (**D**–**E**), 0.1 mm (**F**)

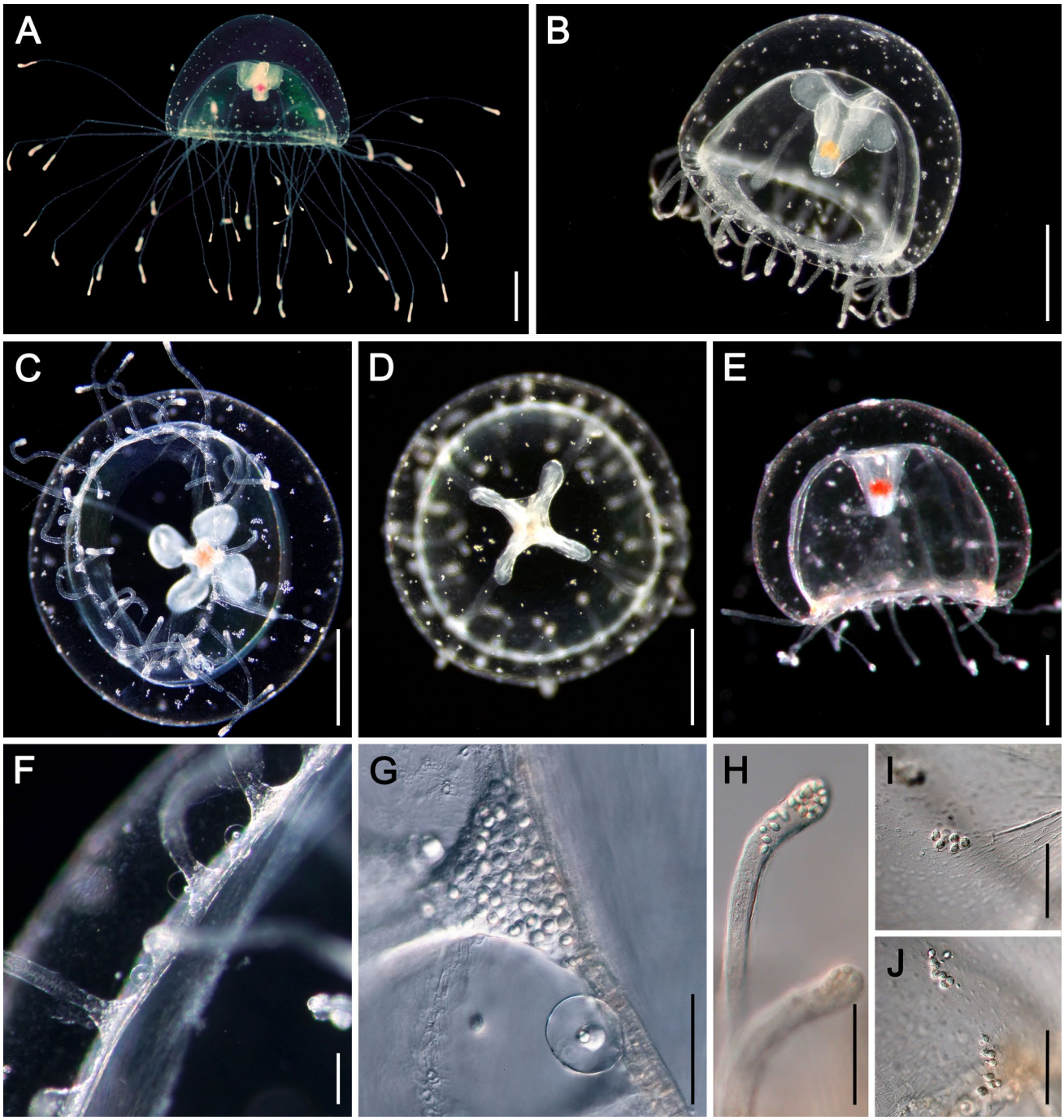

Fig. 2 *Aglauropsis kawari* Moreira & Yamashita, 1972, live specimens. **A** Mature medusa (lateral view) showing exumbrellar nematocysts and overall morphology; **B** Subadult medusa (oblique view), showing the cruciform manubrium with red pigmentation and blade-like, twisted gonads; **C** Oral view of a mature medusa; **D** Aboral view of a subadult medusa; **E** Lateral view of a juvenile medusa; **F** Margin of a mature medusa, showing tentacle insertions and statocysts; **G** Detail of margin showing the base of a tentacle with nematocyst and statocyst containing a single rounded statolith; **H** Detail of a tentacle tip with white, club-shaped terminal swelling; **I–J** Close-ups of exumbrella showing clusters of nematocysts of tentacle insertion types. Scale bars: 1 mm (**A**-**D**), 0.2 mm (**E**), 0.1 mm (**F**-**J**)

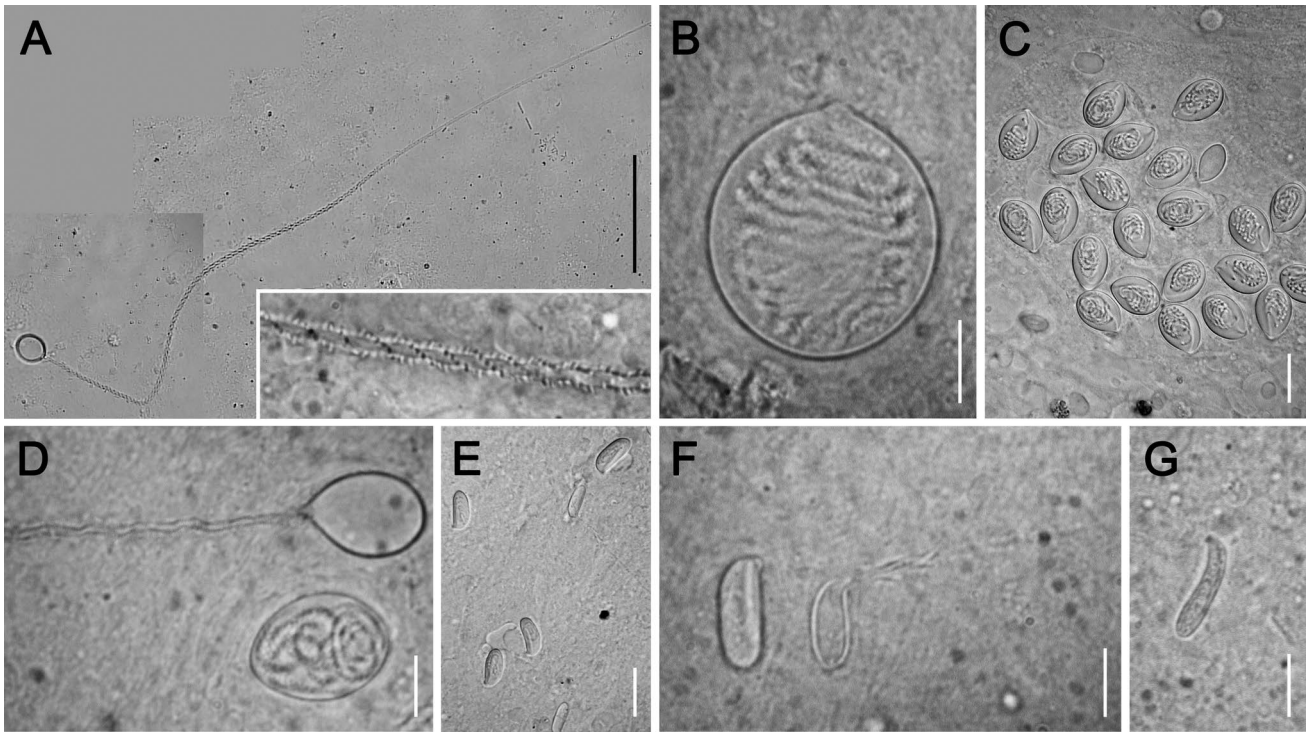

Fig. 3 Cnidome of *Aglauropsis kawari* Moreira & Yamashita, 1972. All nematocysts observed in vivo, from live specimens. **A** Discharged round holotrichous isorhiza from the exumbrella; inset: detail of a tubule armed with short spines; **B** Undischarged round holotrichous isorhiza from exumbrella – note the loosely packed coils of the tubule perpendicular to the main axis of the capsule; **C** Undischarged ellipsoid atrichous isorhiza from tentacle tips; **D** Detail of a discharged and an undischarged ellipsoid atrichous isorhiza; **E–F** Undischarged and discharged microbasic mastigophore from manubrium and tentacle base; **G** Undischarged club-shaped isorhiza. Scale bars: 50 µm (**A**), 5 µm (**B**, **D**, **F**, **G**), 10 µm (**C**, **E**)

Results

Taxonomic characterization

Phylum: Cnidaria Hatschek, 1888
Subphylum: Medusozoa Petersen, 1979
Class: Hydrozoa Owen, 1843
Subclass: Trachylinae Haeckel, 1879
Order: Limnomedusae Kramp, 1938
Family: Olindiidae Haeckel, 1879
Genus: *Aglauropsis* Müller, 1865
Aglauropsis kawari Moreira & Yamashita, 1972
Figures 1, 2, 3, and 4; Tables 2 and 3

Material examined:
Neotype (designated herein): Brazil, Rio Grande do Sul State: 17 October 2018, −32°11.41'S, −52°9.13'W, temperature and salinity not recorded, G.M. Montfort coll. CBS ZOO 000185 (1 specimen).

New material: Brazil, São Paulo State, São Sebastião Channel: 26 January 1999 (coordinates, temperature and salinity not recorded), V.B. Tronolone coll. (1 specimen); 18 August 1999, 23°50.76′S, 45°26.04′W, water-column range temperature 21.35–21.75 °C, salinity 34–35 (measurements at 5–20 m), V.B. Tronolone coll. (3 specimens); 20 August 1999, 23°49.97′S, 45°25.71′W, water-column range temperature 20.55–21.60 °C, salinity 34–35 (5–20 m), V.B. Tronolone coll. (2 specimens); 13 October 1999, near Ilha das Cabras (coordinates not recorded), water-column range temperature 20.60–21.50 °C, salinity 35–36 (5–30 m), V.B. Tronolone coll. (7 specimens); 18 October 1999, near Ilha das Cabras (coordinates not recorded), water-column range temperature 17.95–21.80 °C, salinity 35–36 (5–30 m), V.B. Tronolone coll. (2 specimens); 24 November 1999, 23°49.78′S, 45°25.35′W, water-column range temperature 22.60–22.80 °C, salinity 36 (5–10 m), V.B. Tronolone coll. (2 specimens); 29 November 1999, 23°50.28′S, 45°24.78′W, water-column range temperature 17.65–22.80 °C, salinity 36 (5–30 m), V.B. Tronolone coll. (6 specimens); 17 January 2000, 23°50.48′S, 45°25.01′W, water-column range temperature 20.30–28.50 °C, salinity 35–36 (5–25 m), V.B. Tronolone coll. (1 specimen); 14 February 2000, Farol (coordinates not recorded), water-column range temperature 21.80–26.30 °C, salinity 35–36 (5–15 m), V.B. Tronolone coll. (1 specimen); 12 May 2000,

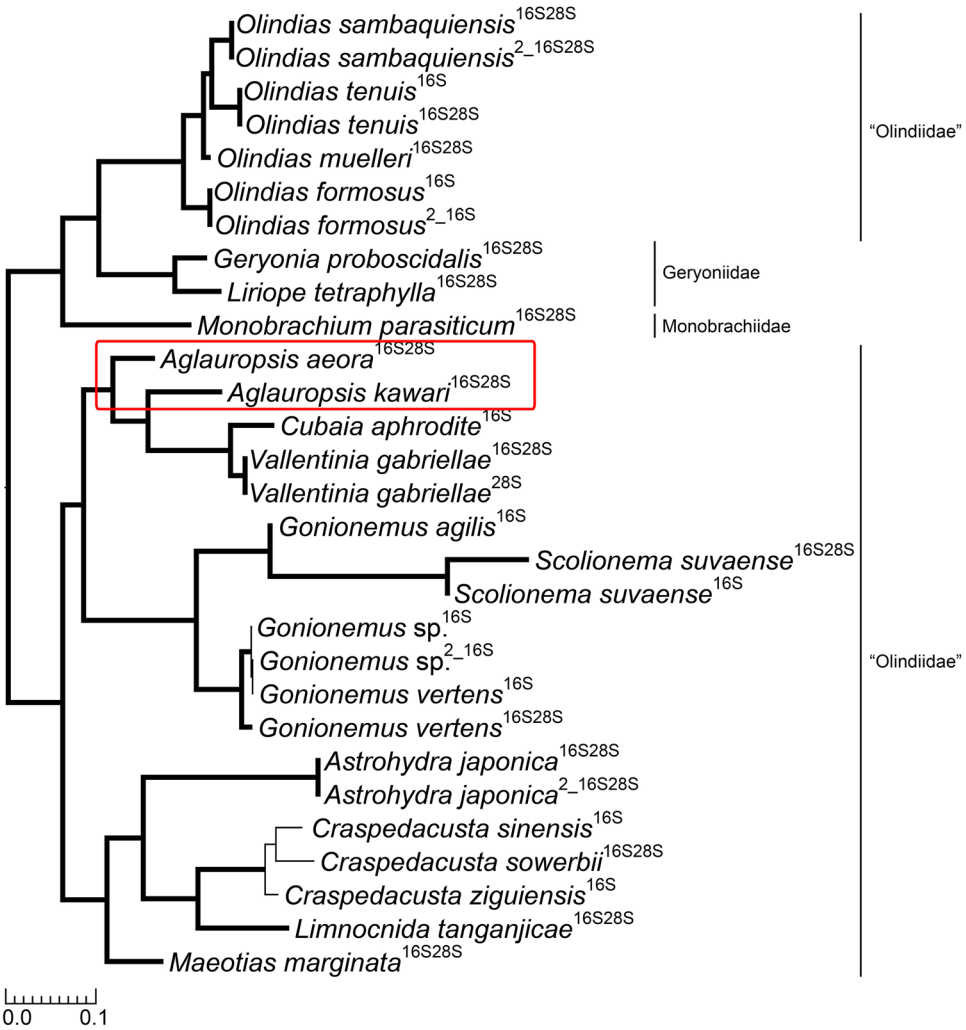

Fig. 4 Maximum Likelihood (ML) phylogenetic tree showing the relationships of *Aglauropsis kawari* within the family Olindiidae. This tree is based on the 16S ribosomal RNA and 28S ribosomal RNA genes. Bold branches indicate high support values. The positions of *A. aeora* and *A. kawari* are highlighted with a red box. Scale bar represents the estimated number of substitutions per site (0.01 branch length units)

Table 2 Morphometric data of *Aglauropsis kawari* Moreira & Yamashita, 1972 medusae at different developmental stages (mature, subadult, and young). All measurements are in millimeters (mm). Data presented as mean (range) ± standard deviation (number of specimens)

	Mature medusae Mean ± SD (range) (n)	Subadult medusae* Mean ± SD (range) (n)	Juvenile medusae Mean ± SD (range) (n)
Maximum diameter	4.08 ± 0.76 (1.88–5.08) (41)	1.85 ± 0.36 (1.44–2.44) (10)	0.95 ± 0.14 (0.80–1.12) (4)
Maximum height	3.33 ± 0.61 (1.36–3.91) (41)	1.37 ± 0.25 (1.00–1.76) (10)	0.75 ± 0.14 (0.68–0.96) (4)
Diameter at margin	3.24 ± 0.71 (1.08–4.33) (41)	1.23 ± 0.31 (0.74–1.88) (10)	0.57 ± 0.08 (0.50–0.68) (4)
Diameter at aperture	2.33 ± 0.58 (0.80–3.41) (40)	0.62 ± 0.19 (0.40–0.88) (9)	0.19 ± 0.08 (0.14–0.28) (3)
Jelly thickness at apex	0.92 ± 0.26 (0.48–1.66) (41)	0.37 ± 0.10 (0.26–0.52) (10)	0.12 ± 0.03 (0.10–0.16) (4)
Manubrium length	0.99 ± 0.21 (0.48–1.25) (41)	0.35 ± 0.14 (0.18–0.60) (10)	0.16 ± 0.05 (0.10–0.20) (4)
Number of marginal tentacles	35 ± 4.8 (25–44) (36)	25.2 ± 5.91 (17–35) (10)	12.5 ± 1.0 (12–14) (4)
Number of statocysts	26 ± 7.0 (13–38) (41)	9.8 ± 4.1 (4–18) (10)	3.7 ± 1.3 (2–5) (4)

* specimens morphologically similar to adults but without gonads

23°50.03′S, 45°24.63′W, water-column range temperature 22.05–25.10 °C, salinity 36 (5–38 m), V.B. Tronolone coll. (13 specimens); 15 May 2000, 23°49.75′S, 45°28.77′W, water-column range temperature 23.95–24.90 °C, salinity 35–36 (5–10 m), V.B. Tronolone coll. (1 specimen); 19 May 2000, 23°50.20′S, 45°25.01′W, water-column range temperature 24.80–25.70 °C, salinity 35–36 (5–30 m), V.B. Tronolone coll. (2 specimens); 10 June 2000,

Table 3 Dimensions and distribution of undischarged nematocyst capsule types identified in *Aglauropsis kawari* Moreira & Yamashita, 1972. Measurements in micrometers. Data presented as Mean ± standard deviation (range) (number of capsules measured)

	Length (µm) Mean ± SD (range) (n)	Width (µm) Mean ± SD (range) (n)
Exumbrella Round holotrichous isorhiza	15.8 ± 0.65 (14.8–16.1) (5)	14.6 ± 0.49 (13.9–15.0) (5)
Tentacle tips and tentacle bulbs Ellipsoid atrichous isorhiza	12.4 ± 0.63 (10.9–13.7) (92)	8.6 ± 0.36 (7.6–9.4) (92)
Umbrella margin and tentacle bulbs Microbasic mastigophore	7.8 ± 0.78 (6.7–9.0) (15)	4.6 ± 0.54 (4.0–5.6) (15)
Manubrium Microbasic mastigophore Club-shaped isorhiza	8.1 ± 0.87 (6.7–9.7) (34) 8.9–9.1 (3)	3.5 ± 0.35 (2.9–4.1) (34) 1.6–2.1 (3)

23°50.32′S, 45°24.95′W, water-column range temperature 19.70–25.40 °C, salinity 35 (5–29 m), V.B. Tronolone coll. (2 specimens); 12 June 2000, 23°50.02′S, 45°25.91′W, water-column range temperature 20.90–24.30 °C, salinity 36 (5–20 m), V.B. Tronolone coll. (9 specimens); 17 June 2000, 23°50.08′S, 45°25.05′W, water-column range temperature 18.60–24.65 °C, salinity 35–36 (5–29 m), V.B. Tronolone coll. (1 specimen); 14 January 2004 (coordinates, temperature and salinity not recorded), (3 specimens), V.B. Tronolone coll.; 3 July 2005 (coordinates, temperature and salinity not recorded), (1 specimen); 30 October 2015 (coordinates, temperature and salinity not recorded), (1 specimen); 4 September 2019 (coordinates, temperature and salinity not recorded), (1 specimen); 12 December 2019 (coordinates, temperature and salinity not recorded), (10 specimens), A.E. Migotto coll. MZUSP 8807; 10 October 2022, 23°50.13′S, 45°25.15′W, temperature 22.5 °C and salinity 33, G.M. von Montfort coll. (5 specimens), GenBank accession numbers: 16S (PZ111969), 28S (PZ111945).

Brazil, Rio Grande do Sul State, 26 December 2012, 32°9.76'S, 52°6.24'W, temperature 24.16 °C, salinity 31.84 and Chl-a 4.08 µg/L, G.M. von Montfort coll. (2 specimens); 24 August 2017, 32°9.76'S, 52°6.24'W (temperature and salinity not recorded), G.M. von Montfort coll. (20 specimens), GenBank accession numbers: 16S (PZ111970), 28S (PZ111946).

Type locality. Off Rio Grande do Sul State, Brazil.

Diagnosis. Medusa hemispherical, with isolated or clustered nematocysts on the exumbrella; with 12–44 marginal tentacles with a white, club-shaped terminal swelling; tentacles of two types according to insertion: at umbrellar margin and above the umbrellar margin; 13–38 closed statocysts with a single statolith. Manubrium and mouth cruciform, mouth simple, smooth. Four small, smooth, blade- to pouch-like gonads extending along the proximal fifth portion of the radial canals, connecting with the manubrium corners.

Neotype description. Umbrella globular, 5 mm wide and high. Four broad radial canals ending in a ring canal (Fig. 1A, B). Manubrium cruciform, approximately 1/3 of the subumbrella; mouth simple, smooth. Gonads pouch-like, slightly twisted, surface smooth, hanging down from the proximal parts of the radial canals, continuous with the upper stomach wall, obscuring manubrium and mouth (Fig. 1D). Gonads approximately half the subumbrellar cavity height. Velum broad, up to 1/3 of the radius of the subumbrellar aperture (Fig. 1C). A total of 44 tentacles, generally alternating in insertion (Fig. 1E), each with an elongated terminal swelling (Fig. 1E). Twenty-two statocysts along the bell margin, usually inserted near the base of tentacles arising from the bell margin or in between the two tentacle whorls (Fig. 1F); each with one statolith.

General description

Mature medusa: Umbrella transparent, hemispherical, 1.3–3.9 mm high, 1.8–5.0 mm wide (Fig. 2A–C, and Table 2). Mesoglea moderately thick, gradually thickening from margin to apex. Exumbrella with isolated nematocysts or clusters/rows of up to ~ 10 nematocysts, typically around a meridional band (Fig. 2B-E) and around tentacle insertions. Four broad, straight radial canals (55–68 µm wide) ending in an equally wide ring canal. Velum broad, opening approximately half umbrella's marginal diameter. Umbrella margin provided with 25–44 marginal tentacles, devoid of marginal bulbs and inserted alternately (though not always) either strictly on the margin and completely free (Fig. 2F) or a short distance above the bell margin and slightly adnate to the exumbrella; both types with approximately the same length; tips with white, club-shaped terminal swellings containing nematocysts (Fig. 2A, C, H), surface entirely flagellated; gastrodermis of tentacles parenchymatous, rosy. Nematocysts scattered or absent along tentacles, concentrated on the club-shaped terminal swellings (Fig. 2H) and bases (Fig. 2G). Margin provided with 13–38 closed statocysts (56–70 µm in diameter), usually inserted near the base of tentacles arising from bell margin or in between the whorls of tentacles, each statocyst bearing centrally a rounded statolith (14–21 µm diameter) (Fig. 2G). Manubrium short, without peduncle, cruciform in cross-section (Fig. 2B), with perradial arms, extending down for about half the bell cavity, with an internal

Table 4. Genetic similarity matrix for ribosomal DNA markers (28S and 16S) among selected Limnomedusae species. The upper right triangle represents 16S similarity percentages, and the lower left triangle represents 28S similarity percentages. NA indicates self-comparison, and "no data" indicates data not available

28S\16S	*Aglauropsis kawari*	*Aglauropsis aeora*	*Vallentinia gabriellae*	*Cubaia aphrodite*
Aglauropsis kawari	**NA**	80.22	78.93	77.83
Aglauropsis aeora	93.27	**NA**	80.17	79.06
Vallentinia gabriellae	93.10	91.47	**NA**	91.63
Cubaia aphrodite	No data	No data	No data	**NA**

gastrodermal red spot towards its lower third (Fig. 2E); mouth simple, lacking folds and a nematocyst ring or batteries. Four simple gonads (Fig. 2A–D) with smooth, flattened, blade-like, twisted surface, not pendant or folded, extending along proximal fifth portion of radial canals, connecting with the manubrium corners; in apical view, propeller-like. Cirri, ocelli, and centripetal canals absent. Coloration in life: subumbrella green (side illumination); tentacle tips white with a rosy core, remaining tentacles transparent; manubrium white with a red spot.

Subadult medusa: Ten individuals observed, all with the same characteristics as the adults (Fig. 2B and Table 2), except: no ripe gonads; smaller umbrellas (diameter: 1.4–2.4 mm; height: 1.0–1.7 mm); fewer marginal tentacles (17–35); fewer statocysts (4–18). Red spot on manubrium present. Nematocyst clusters all over the exumbrella. Mesoglea thick, slightly thicker at apex than laterally.

Juvenile medusa: Umbrella 0.6–0.9 mm high, 0.8–1.1 mm wide (Fig. 2E and Table 2), globular. Nematocyst clusters all over the exumbrella. Mesoglea relatively thin, with uniform thickness. Margin with 12–14 tentacles, arranged as in adults, and 2–5 statocysts. Manubrium short, either without pigmentation or with a bright yellow spot.

Cnidome: Four types of nematocysts identified (Table 3; Fig. 3):

Round holotrichous isorhizas (Fig. 3A – B) (seen discharged), present on exumbrella (Fig. 4), capsule almost spherical, tubule long, spirally barbed and clearly tapering from base to distal end.

Ellipsoid atrichous isorhizas (seen discharged), present on bases and tips of tentacles (Fig. 3C – D) (almost absent along the length of tentacles), capsule drop-shaped, tubule long, spines either inconspicuous or absent in light microscopy.

Microbasic mastigophores (Fig. 3E – F) (seen discharged) present on manubrium and bases of tentacles, capsule bean-shaped; shaft, seen as a rod inside capsule, when discharged provided with long spines and approximately the same length as the capsule itself.

Club-shaped isorhizas (Fig. 3G) (seen undischarged) present on manubrium, rare, capsule thin and long.

Remarks: *Aglauropsis kawari* was described by Moreira and Yamashita (1972) based on 11 male and 10 immature, formalin-preserved specimens collected from surface waters off Rio Grande do Sul State, Brazil. The preservation method used is known to induce umbrella shrinkage, depigmentation, and cnidocyst degradation, potentially altering proportions of morphological features and leading to taxonomic inconsistencies (e.g. Martinez et al. 2013; Schuchert and Collins 2021). Consequently, the original account did not include features only visible in live specimens. In preserved *A. kawari* specimens, for instance, the umbrella became opaque, internal structures turned milky white, and manubrium pigmentation vanished. Tentacle size and posture, as well as umbrella proportions, changed noticeably, with statocysts sometimes becoming inconspicuous. These preservation effects account for missing information on the cnidome composition and coloration in life. Most notably, Moreira and Yamashita assert that the "tentacles issuing above bell margin are about ½ diameter of bell. The others are shorter, about ¼ of diameter of bell". In live specimens we have not seen any consistent differences between the two types of tentacles, except for size variation due to different growth states among tentacles. In preserved specimens, the tentacles are usually contracted, and we have noticed that some of those that are adnate to the exumbrella do look shorter than the free ones, although they are not. Furthermore, exumbrellar nematocysts can become inconspicuous in fixed material and may be abraded in net-collected specimens, as observed in the neotype described here.

The original description did not document juvenile individuals. Since the original report, several records of *A. kawari* have been published (see below), extending its known distribution from Argentina (39.84°S) to São Sebastião, on the coast of São Paulo State (23°49'S). However, these subsequent publications lack cnidome characterization and detailed information regarding living specimens,

and do not provide additional morphological data to complement the original description of the species.

Moreira and Yamashita did not designate a type specimen for *A. kawari*. They stated that all studied specimens were deposited in the collections of the Instituto de Biologia Marinha (currently Centro de Biologia Marinha) of the University of São Paulo. However, this institution has never maintained a formal biological collection. Our attempts to locate these specimens proved unsuccessful, leading to the conclusion that this putative type material is lost. Therefore, the absence of properly deposited type specimens precludes any further reliable taxonomic examination of the original material.

Given the inaccuracies in the original description and to prevent potential future misidentification of the species, we herein designate a neotype. Following Article 75 of the International Code of Zoological Nomenclature (ICZN 1999), the selected specimen is consistent with the original description and was collected from the same locality as the specimens originally studied.

Distribution: The species is known from the continental margin of the Atlantic Ocean in South America, with recorded occurrences from Brazil to Argentina. Its distribution spans latitudes 23.49°S – 39.84°S (Moreira and Yamashita 1972; Girola et al. 1992; Zamponi 1992; Zamponi and Genzano 1994; Migotto et al. 2002; Genzano et al. 2008; Nogueira Jr. et al. 2014; Cruz and Siquier 2019).

Molecular analysis

Genetic similarities were high when considering both molecular markers, but with two major caveats: (i) similarities between congeneric samples representing *A. kawari* (our study) and *Aglauropsis aeora* Mills, Rees & Hand, 1976 (GenBank) were high, typically intergeneric values (80.2% and 93.2% for 16S and 28S, respectively), and (ii) these values were very similar to distances for proximal groups as estimated in the phylogenetic tree (i.e. 78.9% for 16S, 93.1% for 28S *A. kawari* vs *Vallentinia gabriellae* Vannucci Mendes, 1948); see Table 4.

The combined 16S + 28S phylogenetic analysis of Limnomedusae grouped *A. kawari* within a clade that includes *A. aeora* and *Vallentinia gabriellae*, but the genus is not recovered as monophyletic (Fig. 4); similar comparable results are presented in the 16S and 28S gene phylogenies (Supplementary Figs. S1 and S2) and support values related to *A. aeora* and *A. kawari* positions were relatively high. Because we found both molecular markers, nuclear and mitochondrial, with similar evolutionary trends, we can deduce two alternative historical scenarios: relatively old cladogenesis for *Aglauropsis* or relatively high molecular rate changes versus morphology evolution.

Discussion

The genus *Aglauropsis* currently comprises six valid species, each characterized by distinct morphological and ecological traits: *A. aeora* Mills, Rees & Hand, 1976, *A. conanti* Browne, 1902, *A. edwardsii* Pagès, Bouillon & Gili, 1991, *A. jarli* Kramp, 1955, *A. kawari*, and *A. vannuccii* Thomas & Chhapgar, 1975, and one *taxon inquirendum* (*A. agassizii* F. Müller, 1865). A comparative morphological overview of *Aglauropsis* species is presented in Table 5, highlighting primary distinguishing features, such as umbrella size and shape, gonad structure and position, nematocyst arrangement, and manubrium and tentacle morphology.

Aglauropsis kawari shares morphological affinities with *A. jarli* and *A. vannuccii* Thomas & Chhapgar, 1975, particularly in umbrella dimensions (1.3–3.9 mm high and 1.8–5.0 mm wide) and manubrium morphology (cruciform). However, *A. kawari* is uniquely characterized by the absence of distinct nematocyst rings on its tentacles and the presence of isolated or clustered nematocysts on the exumbrella, often arranged in a meridional band. Furthermore, *A. kawari* has a simple mouth, differentiating it from these congeners.

In contrast, *A. conanti* exhibits a larger umbrella (22.0 × 15.0 mm high and 10.0–20.0 × 15.0 mm wide) and curtain-like gonads extending nearly the entire length of the radial canals. *A. conanti* is also distinguished by a mouth provided with large, folded lips with a nematocyst band, whereas *A. kawari* has a simpler, shorter manubrium and smooth, non-pendant gonads.

Aglauropsis edwardsii presents intermediate morphological characters, including gonads extending more than halfway along the radial canals and distal ends pendant. Its smaller, slightly folded lips resemble those of *A. conanti*. However, its overall size (15.0 × 11.0 mm) and the presence of nematocyst rings near the tentacle bases differentiate it from *A. kawari*. Notably, *A. aeora* is currently the sole species with a fully documented life cycle, including the polyp stage, obtained through laboratory rearing by Mills et al. (1976).

The distribution patterns of *Aglauropsis* suggest distinct biogeographical evolutionary histories and environmental adaptations across the genus. In the Southwest Atlantic, our sampling recorded *A. kawari* in waters ranging from 17.65 to 27.50 °C with salinities of 31–36, consistent with tropical and warm-temperate shelf systems. In contrast, congeners associated with higher-latitude or upwelling-influenced regions, such as *A. conanti* from the Falkland Islands and *A. aeora* from the North Pacific coast, exhibit a tolerance for colder thermal regimes. While these disjunct distributions hint at historical diversification driven by environmental gradients, it is important to note that these patterns remain provisional. The lack of standardized abiotic data for many

Table 5 Comparative morphological overview of valid *Aglauropsis* species. Main distinguishing features are listed for umbrella size and shape, number of statocysts, gonad and manubrium structure and position, cnidome, and geographical distribution (adapted from Pagès et al. 1991) ("n.a." = data not available)

Species	Width X height (mm)	Number of tentacles	Number of statocysts	Gonads	Manubrium	Cnidome	Distribution	References
Aglauropsis kawari Moreira & Yamashita, 1972	1.8–5.1 X 1.3–3.9	25–44	13–36	Small, on proximal part of radial canals, near stomach; pouch-like, laterally flattened, slightly oblique to long axis of manubrium	About ½ of the height of bell cavity; 4 short, simple lips	Holotrichous isorhiza (exumbrella): atrichous isorhiza (tentacles) and microbasic mastigophore (manubrium)	South Brazil	This paper, Moreira and Yamashita 1972:271–274, Bouillon 1999
A. aeora Mills, Rees & Hand, 1976	10.0–20.0 X 15.0	180–210	60–100	Curtain-like, transversally lobed, extending almost entire length of radial canals	Hangs down about ½ the length of the bell cavity. 4 large, flared, crenulated lips, bordered by a row of nematocysts	Microbasic eurytheles and isorhizas (tentacles, manubrium and exumbrella)	USA	Mills et al. 1976:23–42, Wrobel and Mills 1998
A. conanti Browne, 1902	22.0 X 15.0	200 in 2–3 rows	More than 50	Curtain-like; extending almost entire length of radial canals	Fairly long, almost all subumbrellar cavity length; 4 large, folded lips with a band of nematocysts	Microbasic eurytheles and isorhizas (tentacles, manubrium and exumbrella)	Falkland Islands, Strait of Magellan	Mayer 1910: 362–363, Kramp 1957: 42, 1959: 176, 1961, Bouillon 1999: 431
A. edwardsii Pagès, Bouillon & Gili, 1991	15.0 X 11.0	110, with rings of nematocysts	46	Curtain-like, extending half of the length of radial canals, distal ends pendent	½ of height of subumbrellar cavity; 4 small, slightly folded lips, bordered with a large band of nematocysts	incompletely known: microbasic eurytheles in manubrial band	Benguela Current, Northern Namibia	Pagès et al. 1991: 94–95, 1992: 35–36, Bouillon 1999: 431
A. jarli Kramp, 1955	4.0 X 4.0	8, with rings of nematocyst throughout	24	Distal ends pendant; on distal half of radial canals	Very small, less than ¼ the subumbrellar cavity length; no distinct lips	n.a	West Africa	Kramp 1955: 267–269, 1959: 176, 1961: 218
A. vannuccii Thomas & Chhapgar, 1975	8.0 X 6.0	28, with rings of nematocyst throughout	24–28	Smooth, sac-like, with distal ends pendant; on proximal ¾ of radial canals	Short, with small, marginally thickened, folded lips	n.a	India	Thomas and Chhapgar 1975, 1979: 588

historical records, such as those for *A. jarli* in West Africa and *A. vannuccii* in India, and the potential for sampling bias in poorly surveyed regions limit our ability to definitively characterize the ecological niche of the entire genus. Following the principles of integrative taxonomy, the synthesis of our new abiotic data with morphological and genetic evidence provides a more robust, yet cautious, framework for understanding the distribution of *A. kawari* in its evolutionary context.

The substantial genetic distances observed between *Aglauropsis* species in our analyses, coupled with documented morphological variation within the group, raise questions regarding the monophyly of the genus. While our data clarify the identity of *A. kawari*, the divergence levels suggest that *Aglauropsis* may encompass multiple distinct evolutionary lineages. However, a formal revision of the genus would require a more extensive phylogenomic approach and broader taxonomic sampling across the Olindiidae to avoid taxonomic instability. Consequently, current generic assignments should be considered provisional until a more comprehensive systematic framework is established. The addition of molecular data from the present paper expands the phylogenetic framework for this genus and provides a foundation for future studies. Continued efforts to sequence additional markers and include more *Aglauropsis* species will be essential for resolving evolutionary relationships and improving the systematic resolution within this understudied genus.

Conclusions

The designation of a neotype for *A. kawari* provides taxonomic stability for the species, anchoring its identity through a detailed morphological diagnosis. This is the first work with a genetic characterization for the species in the Southwest Atlantic and the addition of comprehensive morphological and genetic data significantly advance our understanding of the Olindiidae clade. The integrative approach not only clarifies the identity of the species but also highlights the critical need for a more coordinated research effort into the taxonomy and natural history of Limnomedusae. By providing a robust framework for future comparisons, the study underscores the existing knowledge gaps and reinforces the importance of targeted investigations. Ultimately, such an integrative perspective is vital for unraveling the complex evolutionary history of these lineages, allowing us to transition from isolated descriptions to a more cohesive understanding of the historical drivers that have shaped diversifications across the global oceans.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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Data availability Data generated or analyzed during this study are included in this published article.

Author contribution GMVM was responsible for conceptualization, conducted morphometry and original draft preparation and editing of the manuscript. VBT contributed to the conceptualization of the study, morphometry, and was also involved in the original draft preparation and editing. MMM was responsible for conceptualization, genetic analysis, and review and editing of the manuscript. RMN contributed to conceptualization as well as review and editing. AEM was responsible for conceptualization, morphometry, original draft preparation, editing, and supervision of the work. All the authors read and approved the manuscript.

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