Integrating molecular and morphological evidence revives the blubber jellyfish, *Catostylus purpurus* (Scyphozoa: Rhizostomeae; Catostylidae) of the Indo-Pacific (Philippines)

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Abstract

Jellyfishes have ecological and societal value, but our understanding of taxonomic identity of many jellyfish species remains limited. Here, an approach integrating morphological and molecular (16S ribosomal RNA and cytochrome oxidase I) data enables taxonomic assessment of the blubber jellyfish found in the Philippines. In this study, we aimed to resolve doubt on the taxonomy of *Acromitoides purpurus*, a valid binomen at the time of our research. Our morphological findings confirm that this jellyfish belongs to the genus *Catostylus*, and is distinct from known species of the genus inhabiting the Western Pacific, such as *Catostylus ouwensi*, *Catostylus townsendi*, and *Catostylus mosaicus*. Detailed morphological and molecular analyses of the type specimens from the Philippines with the other *Catostylus* species revive the binomen *Catostylus purpurus* and invalidate *A. purpurus*. Genetic analysis also distinguishes this Philippine jellyfish from *C. townsendi* and *C. mosaicus*. Through this study, we arranged several Catostylidae taxa into *species inquirendae* (*Catostylus tripterus*, *Catostylus turgescens*, and *Acromitoides stiphropterus*) and one *genus inquirenda* (*Acromitoides*) and provided an identification key for species of *Catostylus*. This comprehensive study confirms the blubber jellyfish as *C. purpurus*, enriching our understanding of jellyfish biodiversity. The integration of morphological and genetic analyses proves vital in resolving taxonomic ambiguities within the Catostylidae family and in the accurate identification of scyphozoan jellyfishes.

Introduction

Jellyfishes are prominent invertebrates, and they serve immense socio-economic and ecological roles in shaping the oceans and human well-being (Pitt and Purcell, 2009; Doyle *et al.*, 2014). Many jellyfish species form spectacular blooms, which can influence biogeochemical cycling, including the carbon cycle (Doyle *et al.*, 2014). Because jellyfish aggregations contain organic matter, they also can regulate climate through carbon sequestration, a factor in controlling atmospheric temperature (Doyle *et al.*, 2014; Wright *et al.*, 2021). Jellyfish are also important to people through a variety of seemingly intricate interactions between jellyfish and humans. Specifically, humans are fascinated with jellyfish because they evoke a positive aesthetic appreciation while at the same time discomfort because they inflict stings (Pitt and Purcell, 2009; Doyle *et al.*, 2014) with microscopic capsular organelles equipped with harpoons called nematocysts (Arai, 1997; Pitt and Purcell, 2009; Jarms and Morandini, 2019). At the same time, several scyphozoan jellyfish species (phylum Cnidaria; class Scyphozoa) are edible and support significant fisheries, demonstrating their economic importance (Pitt and Purcell, 2009; Brotz, 2016; Brotz *et al.*, 2017). Despite recognizing their ecological and societal value, our understanding of the taxonomic identity of many jellyfish groups, such as scyphozoans, remains limited (Lawley *et al.*, 2021; Gamero-Mora *et al.*, 2022; Santander *et al.*, 2022). This gap in knowledge is particularly concerning in light of current environmental stressors like climate change, ocean warming, and aquatic pollution (Joppa *et al.*, 2016; Girardello

et al., 2018). As these environmental stressors intensify, clarifying the taxonomy of jellyfish has become extremely critical (as in Girardello et al., 2018; Thomson et al., 2018; Sandall et al., 2023).

One group of particularly prominent scyphozoans is the blubber jellyfishes (genus *Catostylus*) of the order Rhizostomeae with hemispherical bells shaped by thick mesoglea and oral arms with lace-like surfaces (Mayer, 1910; Arai, 1997; Jarms and Morandini, 2019). Like other rhizostomes, blubber jellyfishes have a bell with no prominent mouth on the underside, but rather microscopic openings on each gelatinous arm, through which food is passed to the stomach (e.g. *Catostylus* spp.; see Figure 1A–G; Dawson, 2005a; Boco et al., 2014). They also have nematocysts on their oral arms that enable capture of prey such as zooplankton (Peach and Pitt, 2005;

Dawson, 2005a; Boco et al., 2014). *Catostylus mosaicus* (Quoy & Gaimard, 1824), a well-known blubber jellyfish, occurs along the Australian eastern and southern coasts, where it forms large swarms of medusae in estuaries (Dawson, 2005a; Figure 1A). The colour of the medusae may vary depending on the location of this jellyfish. In Sydney's (Australia) waters, they are usually white or brown, while they are mostly blue in northern Australia (Pitt and Kingsford, 2000; Dawson, 2005a). Their medusae also have a mild sting that inflicts pain but does not pose serious risk to humans (Williamson et al., 1996). Despite their capacity to inflict mild envenomation in humans, blubber jellyfishes remain a crucial component of marine biodiversity (Boco et al., 2014; Browne et al., 2017; Gueroun et al., 2021). Thus, further research into their systematics is vital.
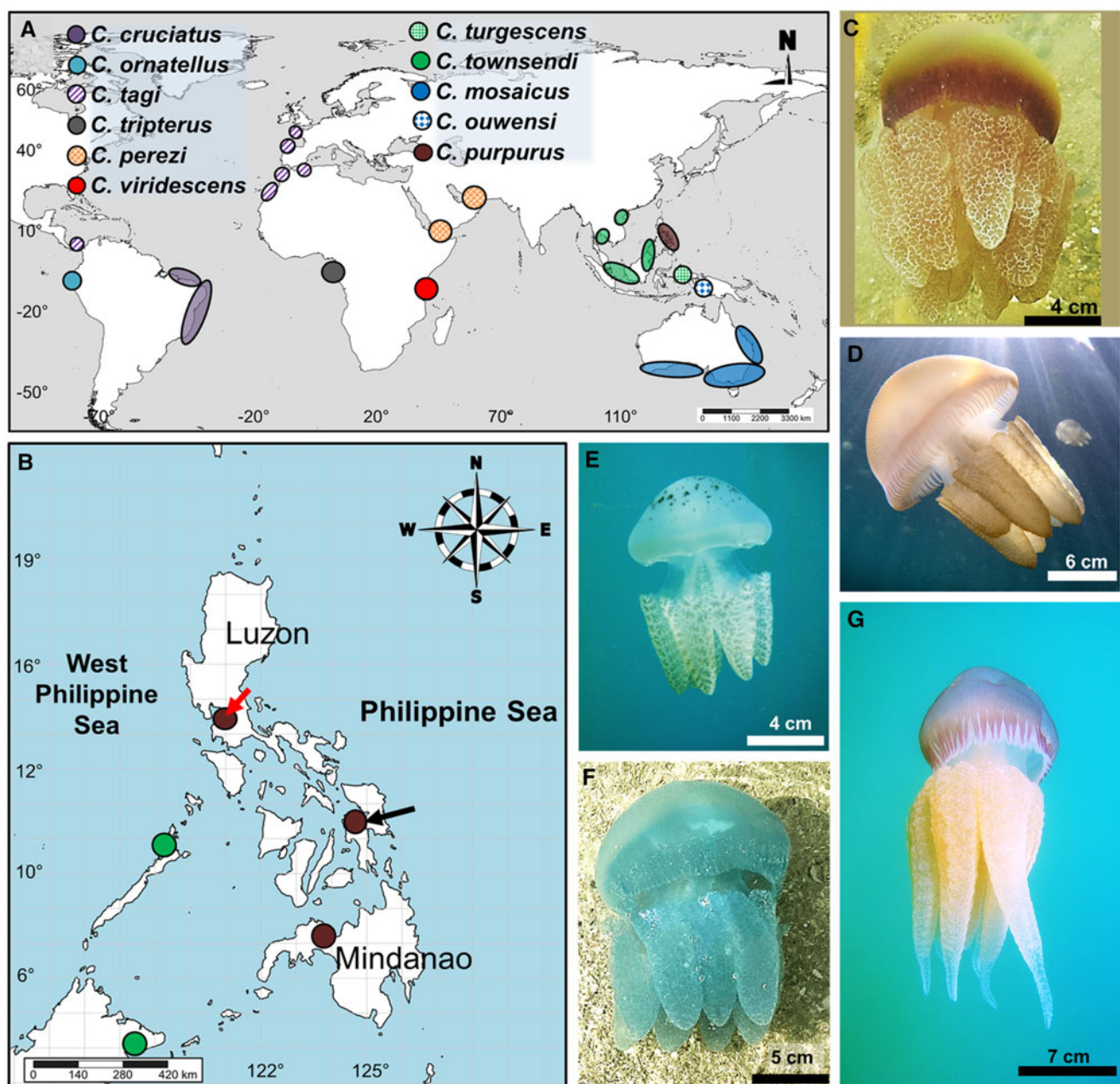
Figure 1. Distribution and images of *Catostylus* spp.: (A) global distribution of species of *Catostylus* (see colour and pattern legends), (B) localities of *Catostylus* spp. in the Philippines (green dot = *C. townsendi*; brown = *C. purpurus*; red arrow = type locality; black arrow = new specimen collections), (C) medusa of *C. purpurus* from central Philippines, (D) *C. mosaicus* from Manly, northern Sydney, Australia, (E) *C. townsendi* from Narra town, Palawan, Philippines, (F) *C. perezi* from Ras Al-Khaimah, United Arab Emirates, and (G) *C. tagi* from Cascais coast in Lisbon, Portugal. Photos courtesy of J. Turnbull (D), A. Galindez (E), M. Gardner (F), and C. Fletcher (G).

Blubber jellyfishes, such as *C. mosaicus* (Quoy & Gaimard, 1824) and *Catostylus tagi* (Haeckel, 1869), play crucial roles in marine ecological processes, including nutrient cycling and transport (West *et al.*, 2009; Wright *et al.*, 2021). Although their exact contributions to transfer of nutrients in the marine food web are yet to be quantified, they serve as a food source for various species, notably turtles (Limpus *et al.*, 2013). For instance, the leatherback turtle, *Dermochelys coriacea* and the green sea turtle, *Chelonia mydas* feed on *C. mosaicus* medusae in Australia (Limpus *et al.*, 2013; Bjorndal, 1997). This highlights the ecological significance of these cnidarians in the context of nutrient cycling and as a critical link in the food chain. Further, the importance of blubber jellyfish extends beyond ecological roles because they are a valuable commodity in coastal societies such as those in Australia and Portugal (Edelist *et al.*, 2021). For example, in Tagus, Portugal, *C. tagi* is harvested for food, pharmaceutical purposes, and animal feed during the jellyfish fishing season in October (Edelist *et al.*, 2021). These multifaceted benefits to ecosystems and societies underscore the importance of understanding the fundamental biology of these jellyfishes, including their taxonomic identity.

Jellyfishes of the family Catostylidae occur in the Philippines, a region of the Coral Triangle with high marine biodiversity richness (Boco and Metillo, 2018; Pinheiro *et al.*, 2019; Gamero-Mora *et al.*, 2022; Figure 1A, B). Scientific literature indicates occurrence of *C. mosaicus* in the region (Light, 1921; Omori and Nakano, 2001; Jarms and Morandini, 2019) going back to the report of one medusa, collected from southwestern Philippines in 1908, i.e. in Malampaya River, Palawan (Mayer, 1915). The jellyfish was speculated to be an immature individual of *C. mosaicus*. However, our extensive surveys for jellyfish in the Philippines since 2013, combined with social media and verified records of jellyfish from the citizen-science project, The Philippine Jellyfish Stings, have not revealed medusae of *C. mosaicus* (whether juvenile or mature) in the territory (Boco *et al.*, 2014; Boco and Metillo, 2018; de Vera-Ruiz, 2022; Boco *et al.*, unpublished). The Philippine Jellyfish Stings citizen-science platform (https://rb.gy/77wnb and https://rb.gy/9wey1) successfully aids in recording occurrences of jellyfish, including blubber jellyfishes, in any part of the region, which led to documentation of occurrences of *Catostylus townsendi* Mayer, 1915 in southwestern Philippines, i.e. Palawan islands (Sabillo, 2020; Boco *et al.*, unpublished data; Figure 1B; Table S1, Supplementary materials). Further, the Philippine blubber jellyfish (not *C. townsendi*) with populations of several morphs such as blue and burgundy is currently being identified as *Acromitoides purpurus sensu* Stiasny (see Boco and Metillo, 2018). Prior to Stiasny's erection of the genus *Acromitoides* in 1921, this species was originally described as *Catostylus purpurus* Mayer, 1910, and indeed, examinations of fresh medusae (without preservation) reveal that the jellyfish fits into *Catostylus* (Boco and Metillo, 2018). The medusae have gastrovascular canal systems showing an anastomosing network, which connects to both rhopaliar and inter-rhopaliar canals (Boco *et al.*, 2014; see Figure 2E in Boco and Metillo, 2018), unlike the canal system of the genus *Acromitoides* (Stiasny, 1921) but in agreement with that of *Catostylus*. Examination of additional specimens of this Philippine blubber jellyfish including museum-preserved medusae can help assess the taxonomy of this rhizostome jellyfish.

While morphological features of scyphozoans aid in identifying jellyfish species by eye, characters in their genomes also provide insights on their phylogenetic histories, clarifying species boundaries and taxonomic classifications (Gamero-Mora *et al.*, 2022; Santander *et al.*, 2022). For example, molecular approaches in the identification of jellyfish, such as by using cytochrome oxidase I marker, effectively aided identification of species in the family Catostylidae, e.g. *Acromitus* sp. (Gómez Daglio and

Dawson, 2017). An even more effective approach in jellyfish taxonomy, uses integrative systematics which combines morphological data and genetic information in identifying scyphozoan jellyfishes, e.g. the upside-down jellyfish *Cassiopea* spp. (Gamero-Mora *et al.*, 2022; Santander *et al.*, 2022). Here, we aimed to describe and clarify the taxonomy of a blubber jellyfish in an Indo-Pacific region using a combination of morphological and genetic information. We hypothesized that the blubber jellyfish with populations of different colour morphs in the Philippines does not belong to genus *Acromitoides*, but instead should be classified among species of the genus *Catostylus*.

Materials and methods

Type specimens and new collections

Specimens labelled *A. purpurus* and *C. purpurus* were examined in the Museum of Comparative Zoology (MCZ) – Harvard University (the USA; *n* = 1 medusa) and Naturalis Biodiversity Centre (RMNH; *n* = 2). See also Table 1. Medusae (*n* = 16) were obtained from various coastal waters in the Philippines during April and July, from 2014 to 2016 and 2022 (see Table 1). They were collected by hand and carefully placed in a plastic bucket filled with filtered seawater to prevent damage to the specimens. In addition, *in-situ* observations (obs.), photographs, and examination of morphology of live specimens of jellyfish in Manila Bay (Cavite province; June 2016) and Visayan Sea, i.e. Bantayan Island of Cebu province (August 2023) in the Philippines were made (Table 1).

Morphological examination

The following morphological features of the medusae (newly collected and type specimens, Table 1) were examined: bell shape, colour, and texture; absence or presence of colour spots or bands on bell; form and texture of marginal lappets including rhopaliar lappets; ostium shape and width; presence or absence and form of subgenital papillae; form, colour and texture of oral arms; absence or presence of appendages connected to the bell or oral arms; and form or shape and position of rhopalia (as in Dawson, 2005*a* and Boco *et al.*, 2014). Sizes of body features like oral arm length and ostium width of the medusae were measured using a metal caliper with 0.1 mm accuracy. Here, the gastrovascular canal system of the medusae, freshly collected, were examined by staining them using a carotene-based pigment, i.e. food dye, and by describing the morphology of the stained canal system, following Boco *et al.* (2014) and Stiasny (1924*b*). The arrangement of the canal system aids identification of the genus (Stiasny, 1924*b*; Thiel, 1978). Voucher specimens were deposited at the National Museum of the Philippines (NMP) and Invertebrate Biology Museum of the University of the Philippines Diliman (UP-DIM).

The jellyfish specimens were identified using the descriptions and images of medusae in Schultze (1897), Mayer (1910), Light (1914, 1921), Stiasny (1920, 1921, 1924*b*, 1925, 1929), Kramp (1961), Heeger (1998), Dawson (2005*a*, 2005*b*), Gul and Morandini (2013), Boco *et al.* (2014), Boco and Metillo (2018), and Jarms and Morandini (2019). Newly collected medusae (from 2014 to 2022) were identified and compared to other *in-situ* observations and images of jellyfish for differential diagnosis. The jellyfish were compared to a confirmed record of *Crambione mastigophora* Maas, 1903 from a bloom in April 2020 in Palawan, southwestern Philippines (Figure S1, Supplementary materials); *Crambionella orsini* Vanhöffen, 1888 in Wasin, Kenya (https://www.inaturalist.org/observations/39918901; Wasini observations, *n* = 2); *C. mosaicus* in Sydney, Australia (https://tinyurl.com/4yhjfnta; J. Turnbull observations,

Table 1. Records of preserved specimens and *in-situ* observations (obs.) of medusae of *C. purpurus*

Locality	Collection date	Latitude	Longitude	Source	Accession codes
Navotas city	9 December 1907	14°34′46.8″N	120°58′00.2″E	Paratype; Mayer (1910)	USNM 27934
Navotas city	11 March 1908	14°40′12.0″N	120°55′12.0″E	Holotype; Mayer (1910)	USNM 27980
Cavite city	2 July 1909	14°30′00.0″N	120°49′48.0″E	Paratype; Mayer (1910)	USNM 28723
Cavite city	2 July 1909	14°30′00.0″N	120°49′48.0″E	Paratype; Mayer (1910)	MCZ IZ: CNID-1807
Manila Bay	1912	14°33′01.1″N	120°58′21.2″E	Paratype; Light (1914)	USNM 38021
Pasay Beach	October 1913	14°31′55.8″N	120°58′41.5″E	Light (1914) description	n. a.
Manila Bay	June 1920	14°32′47.6″N	120°58′42.9″E	Light (1921) description	n. a.
Manila Bay	December 1922	14°32′56.5″N	120°58′33.1″E	Topotype; Stiasny (1924b)	RMNH.COEL.5027
Manila Bay	December 1922	14°32′56.5″N	120°58′33.1″E	Topotype; Stiasny (1924b)	RMNH.COEL.5028
Panguil Bay	December 2013–July 2014	8°06′56.0″N	123°51′49.6″E	*In-situ* obs.; Boco et al. (2014)	n. a.
Panguil Bay	30 August 2014	8°06′56.0″N	123°51′49.6″E	*In-situ* obs.; Boco and Metillo (2018)	n. a.
Panguil Bay	16 November 2014	8°06′56.0″N	123°51′49.6″E	*In-situ* obs.; Boco and Metillo (2018)	n. a.
Iligan Bay	2 August 2014	8°11′14.9″N	124°08′01.6″E	*In-situ* obs.; Boco and Metillo (2018)	n. a.
Carigara Bay	15 June 2014	11°20′19.9″N	124°45′19.1″E	*In-situ* obs.; Boco and Metillo (2018)	n. a.
San Miguel, Leyte	14 June 2014	11°23′8.2″N	124°48′ 24.93″E	*In-situ* obs. and preserved specimens	UPDIM-SCY024-002
San Miguel, Leyte	14 June 2014	11°23′8.2″N	124°48′24.93″E	*In-situ* obs. and preserved specimens	UPDIM-SCY024-003
Marabut, Samar	26 April 2015	11°12′52.01″N	125°10′53.03″E	*In-situ* obs. and preserved specimens	UPDIM-SCY025
Naic, Cavite	04 June 2016	14°20′34″N	120°46′37.0″E	Photographs and *in-situ* obs.	n. a.
Albay, Philippines	27 May 2017	12°59′23.9″N	123°28′36.0″E	Fresh specimens; Regalado and Ramirez (2019)	n. a.
Naval, Biliran	15 June 2016	11°31′20.1″N	124°25′08.8″E	*In-situ* obs. and preserved specimens	UPIM-SCY002
Cabucgayan, Biliran	21 May 2016	11°28′27.4″N	124°34′59.2″E	*In-situ* obs. and preserved specimens	NMP2017C-06
Carigara, Leyte	9 July 2016	11°18′16.2″N	124°40′52.3″E	*In-situ* obs. and preserved specimens	NMP2017C-03
Carigara, Leyte	9 July 2016	11°18′16.2″N	124°40′52.3″E	*In-situ* obs. and preserved specimens	NMP2017C-04
Carigara Bay	9 July 2016	11°19′10.0″N	124°43′07.5″E	*In-situ* obs. and preserved specimens	UPDIM-SCY011
Babatngon, Leyte	16 July 2016	11°25′17.0″N	124°54′09.7″E	*In-situ* obs. and preserved specimens	NMP2017C-08
Marabut, Samar	17 July 2016	11°12′19.4″N	125°10′47.8″E	*In-situ* obs. and preserved specimens	UPDIM-SCY006
Catbalogan, Samar	24 July 2016	11°45′30.1″N	124°53′01.3″E	*In-situ* obs. and preserved specimens	UPDIM-Cni-Scy-013-001
Catbalogan, Samar	24 July 2016	11°45′30.1″N	124°53′01.3″E	*In-situ* obs. and preserved specimens	UPDIM-Cni-Scy-013-002

Location	Date				
Bataan, Luzon	20 April 2019	14°35'06.2"N	120°35'29.2"E	Photographs and videos	n. a
Barugo, Leyte[a]	16 July 2022	11°19'10.0"N	124°43'07.5"E	In-situ obs. and preserved specimens	NMP-8035
Barugo, Leyte[a]	16 July 2022	11°19'10.0"N	124°43'07.5"E	In-situ obs. and preserved specimens	NMP-8036
Barugo, Leyte[a]	16 July 2022	11°19'10.0"N	124°43'07.5"E	In-situ obs. and preserved specimens	NMP-8037
Barugo, Leyte[a]	16 July 2022	11°19'10.0"N	124°43'07.5"E	In-situ obs. and preserved specimens	NMP-8038
Bantayan Island, Cebu	29 June 2023	11°15'55.24"N	123°42'50.48"E	Video	n. a
Bantayan Island, Cebu	21 August 2023	11°11'45.2"N	123°46'37.6"E	Photographs and in-situ obs.	n. a
Bato, Leyte	6 September 2023	10°19'36.93"N	124°47'12.56"E	Photographs and videos	n. a

n. a., not applicable; USNM, Smithsonian National Museum of Natural History, USA.
[a]Tissue was collected for molecular analyses.

$n = 2$); *C. townsendi* observed in June 2018 (A. Galindez observations, $n = 4$ photo, $n = 2$ video) and 1 April 2023 (A. Schilde observations, $n = 2$ photos), both in Palawan, Philippines (Table S1, Supplementary materials); *Catostylus perezi* Ranson, 1945 of United Arab Emirates (https://www.inaturalist.org/observations/52027645; M. Gardner observations, $n = 2$), and *C. tagi* in Portugal (https://www.inaturalist.org/photos/24990680; C. Fletcher observations, $n = 1$).

In 2015, the citizen-science project with a social media platform, The Philippine Jellyfish Stings (https://rb.gy/77wnb; https://rb.gy/9wey1), was established to precisely locate records of jellyfish in the region. Observations including photos and videos of blubber jellyfish published in the page 'Philippine Jellyfish Stings' since 2015–2023 were manually searched, downloaded, and recorded from the social media platform. Contributors of the observations with photographs or videos of jellyfishes in the project were contacted when needed to obtain details related to these jellyfish observations such as GPS coordinates or nearest village and landmarks where the jellyfish was recorded (which provided a maximum of $30\,m^2$ resolution of the location of the jellyfish), date and time of observations, and estimated sizes (e.g. bell diameter) of the jellyfish.

Occurrences of the blubber jellyfish medusae and their blooms among several biogeographic regions (i.e. ecoregions) in the Philippines were recorded using *in-situ* observations and citizen-science observations, described above. Locations and names of these ecoregions, e.g. Visayan region, were based on Nañola *et al.* (2011). Further, citizen-science photographs and videos of blooms of *Catostylus* sp. in Bataan, Luzon (20 April 2019; northern Philippines) and Canigao Channel in town of Bato, Leyte in central Philippines (6 September 2023; Table 1) were obtained and, then, compared to our *in-situ* records of blooms of this blubber jellyfish to determine whether the blooms recorded using citizen science belong to the species we observed *in situ*. We compared these citizen-science records of blooms to the appearance of the blooms of *Catostylus* sp. near Cavite (Manila Bay), off Barugo and Carigara towns (Carigara Bay), Bantayan Island, Cebu (Visayan Sea) (see coordinates in Table 1); blooms of *C. townsendi* at Palawan, Philippines (A. Galindez observations in June 2018; P. Dimalaluan observations in February 2019; A. Schilde observations in April 2023) and those in Trat province, Thailand (Marine and Coastal Resources Research and Development Centre; Table S1, Supplementary materials); and a bloom of *C. mosaicus* near Sydney, Australia (J. Turnbull observations).

Interviews ($n = 43$) with prior informed consent were conducted in Biliran, Leyte, and Cebu provinces to record local names of the jellyfish in several Philippine languages like Waray and Cebuano. Names of the medusae were verified using orthographic sources by Rubino (2004), Polistico (2017), and Corpora Project's Waray dictionary (https://corporaproject.org; see Oyzon and Fullmer, 2014). Furthermore, the etymology of this jellyfish in this study was summarized using the references of Mayer (1910), Yang *et al.* (2018), and Bizuneh (2021).

Reported symbionts of the jellyfish *A. purpurus* were identified using taxonomic references of Hartog (1888), Wilson (1911), Boco *et al.* (2014), and Boco and Metillo (2018). We also adapted an identification key for the species of *Catostylus* by referring to the taxonomic guides of Mayer (1910), Stiasny (1921), Kramp (1961), Kitamura and Omori (2010), Boco *et al.* (2014), and Jarms and Morandini (2019, 2023).

Molecular analyses

Pieces of tissue, each measuring $1\,cm^2$, were collected from the marginal lappets of each of the four specimens from Carigara

Bay (near Barugo town, Leyte Island) and preserved in 99% ethanol in July 2022 (museum accession codes: NMP-8035 to 8038, Table 1). After tissue collection, the medusae were morphologically examined while fresh. They were then preserved in 4% formaldehyde solution in seawater and deposited in Philippine museums (accession codes listed in Table 1). Tissues were collected from several colour morphs (one burgundy, two blue and one white) to account for possible mild genetic variation among morphs. Genomic DNA of the jellyfish was extracted using the protocol which substitutes sodium chloride and absolute ethanol for ammonium acetate and isopropyl alcohol (Miller *et al.*, 1988; Nishiguchi *et al.*, 2002). Two genetic markers from the mitochondrial genome, namely cytochrome c oxidase subunit I (*cox1*) and 16S ribosomal DNA (16S), were amplified using the primers med-cox1-F (5′-ACNAAYCAYAAAGATATHGG-3′) and med-cox1-R (5′-TGGTGNGCYCANACNATRAANCC-3′) for *cox1*, and med-rnl-F (5′-GACTGTTTACCAAAGACATAGC-3′) and med-rnl-R (5′-AAGATAGAAACCTTCCTGTC-3′) for 16S (Lawley *et al.*, 2016). Each polymerase chain reaction (PCR) sample was carried out with GoTaq® DNA Polymerase (Promega) in a total volume of 25 μl, containing 50 ng of DNA template and following the manufacturer's instructions. Both genes had the same thermocycling conditions, including an initial denaturation step at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 51°C for 30 s, and 72°C for 1 min, and a final extension step at 72°C for 7 min, followed by holding at 4°C.

PCR success was confirmed by running the samples on a 2% agarose gel, and the samples were purified using Agencourt AMPure XP (Beckman Coulter). We used the BigDye™ Terminator v3.1 Cycle Sequencing Kit (ThermoFisher Scientific) to prepare the sequencing samples, with 1 μl of BigDye reaction mix for each. The samples were sequenced in a 3730 ThermoFisher sequencing machine at Gate Lab (https://gatelab.ib.usp.br/), and chromatograms were assembled using CodonCode Aligner software (CodonCode Corporation, Dedham, MA). The newly generated sequences were deposited in GenBank and their accession codes are PP786537–PP786540 for *cox1* and PP789084–PP789087 for 16S.

Sequenced chromatograms were aligned using CLUSTAL W. Subsequently, phylogenetic trees for *cox1* and 16S were constructed using maximum-likelihood under bootstrap method (as in Gómez Daglio and Dawson, 2017) in the Molecular Evolutionary Genetics Analysis 7 (MEGA7) program. The tree was drawn to scale, with branch lengths measured in the number of substitutions per site. These phylogenetic analyses included eight nucleotide sequences for each marker (*cox1*; 16S such as those from four Philippine Catostylidae medusae and sequences from GenBank for *cox1*, i.e. *C. mosaicus* (AY737247), *C. townsendi* (MN395694), *Acromitus flagellatus* (MN395692), *Mastigias papua* (MN107722), and for 16S, i.e. *C. mosaicus* (KY610585), *C. townsendi* (KY610587), *A. flagellatus* (KY610576), and *M. papua* (KY610621). Sequences of *M. papua* and *A. flagellatus* were used as outgroups. Then, uncorrected pairwise *p*-distances were obtained using the program Geneious. Sequences from these eight samples were further examined by analysing phylogenetic relationships using the plugin FastTree (Price *et al.*, 2010) in Geneious Prime 2024 with all available *cox1* and 16S sequences of *Catostylus* in GenBank (see accession codes in Figures S3 and S4, Supplementary materials). Percent identity of our *Catostylus* sp. sequences were calculated using NCBI's Basic Local Alignment Search Tool (BLAST) which revealed the jellyfish belongs to family Catostylidae as in Gómez Daglio and Dawson's (2017) method.

Results

SYSTEMATICS

Class SCYPHOZOA Goette, 1887
Subclass DISCOMEDUSAE Haeckel, 1880
Order RHIZOSTOMEAE Cuvier, 1800
Family CATOSTYLIDAE Claus, 1883
Genus *Catostylus* Agassiz, 1862
Catostylus purpurus Mayer, 1910
(Figures 1C; 2A–C; F, G; 3A–C; E–I)

Catostylus purpurus: Mayer (1910): 671–672, original description; Light (1914): 207–209, description; Mayer (1915): 187–188, description; Mayer (1917): 213–214, description; Light (1921): 41–42, description; Totton (1921): 9, mention; Chiu (1954): 56, mention; Southcott (1963): 57, sting record; Cleland and Southcott (1965): 107, 158, sting potential; Williamson *et al.* (1996): 213, sting; Heeger (1998): 314–315, brief description.

Acromitoides purpureus: Stiasny (1921): 137–138, brief description, genus change; Stiasny (1924*b*): 39–45, description; Stiasny (1926): 246, mention.

Acromitus purpurus: Thiel (1978): 286, mention [misspelling of genus].

Acromitoides purpurus: Kramp (1961: 368, diagnosis); Kramp (1965: 271, brief description); Cleland and Southcott (1965): 261, mention; Raupp *et al.*, (1996): 49, Table 1, sting potential; Williamson *et al.* (1996): 214, mention; Kitamura and Omori (2010): 114, mention; Boco and Metillo (2018): 71, 74, 76, associations; Muffett and Miglietta (2021): 4, mention; Jarms and Morandini (2019, 2023): 554–555, description; Santhanam (2020): 81, 294, brief description, venomosity; Hwai *et al.* (2021): 67–68, brief description.

Catostylus sp. – Boco *et al.* (2014): 63–77, abundance and associations; Regalado and Ramirez (2019): 531, 534, association with marine fungi; Muffett and Miglietta (2021): 5, mention.

Materials examined

Type specimens

One medusa (paratype) in the MCZ (accession code, a.c.: MCZ IZ: CNID-1807), coast of Cavite city; all are burgundy morphs; two preserved medusae (topotypes) in RMNH (a.c.: RMNH.COEL.5027), unidentified location in Manila Bay, likely Pasay coast. See Table 1 for the dates of collection, and localities of these type specimens.

Additional materials

Sixteen fresh specimens from several localities in the Philippines, which were subsequently preserved in phosphate-buffered 4% formalin: two juveniles and 14 mature medusae, majority are burgundy morphs (2 blue, 1 orange, and 1 white colour morphs were also examined), collectors: C. Capidos, S. R. Boco, and D. Talacay (see Table 1); photographs and *in-situ* observations, Manila Bay (Cavite province), Philippines, observer: S. R. Boco, 4 June 2016; photographs (*n* = 2) and a video, observed near Capinpin Port in Orion, Bataan, Philippines, observer: A. Manlangit; video of the medusa with ectosymbiont fish in Orion, Bataan, observer: J. Gervacio, August 2022; fresh medusae (*n* = 2, not preserved), photographs (*n* = 4) and *in-situ* observations of medusae and a bloom by C. Capidos, Bantayan Island in central Philippines (Table 1); photographs of a blue and burgundy blubber jellyfish (*n* = 5) currently identified as *C. mosaicus* obtained from an unidentified location in the Philippines,
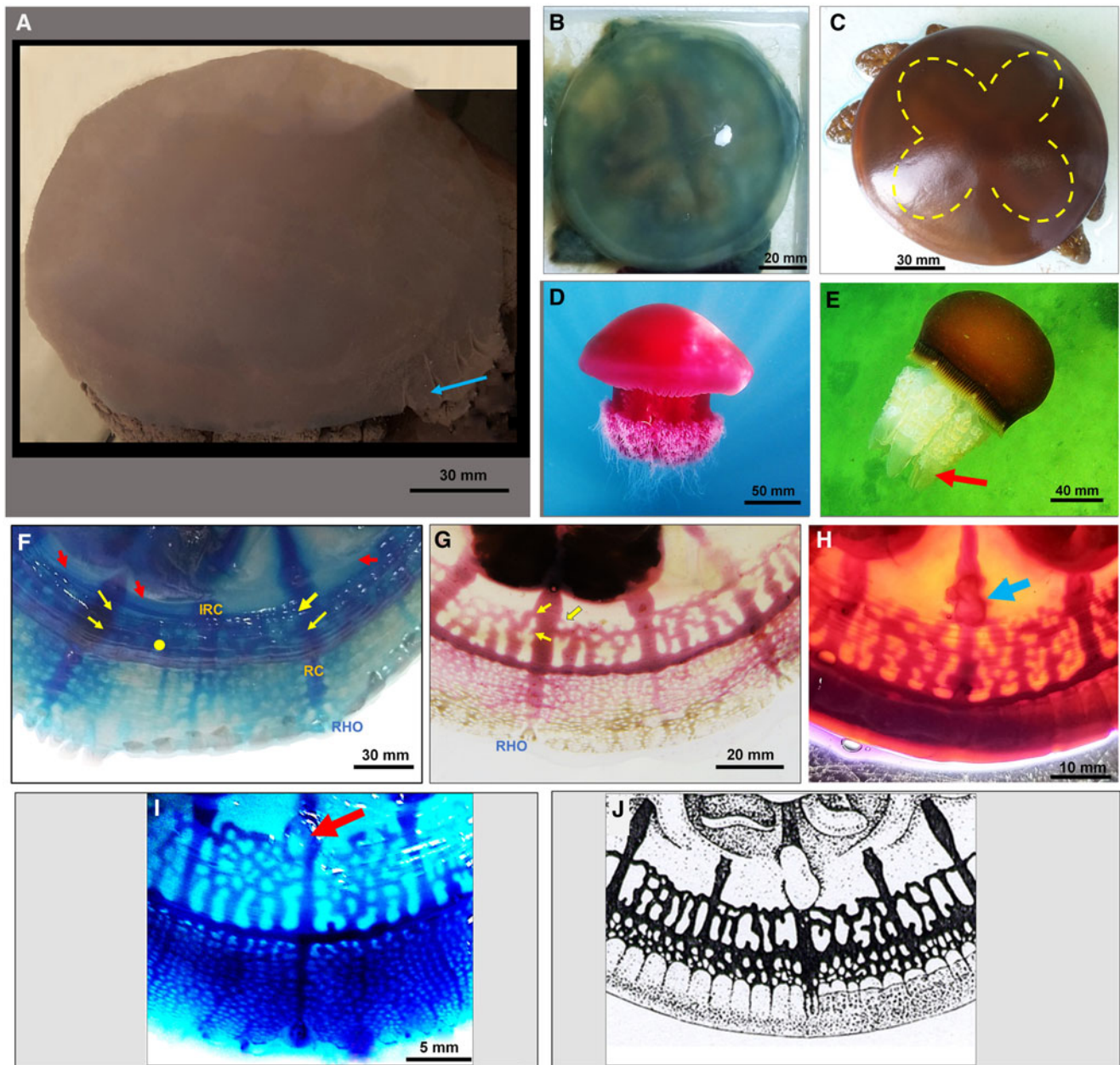
Figure 2. Medusae of *C. purpurus* and morphological features of other species: (A) exumbrella of the topotype (museum accession code, a.c.: RMNH.COEL.5027, Table 1) collected from Manila Bay. Blue arrow = lappet; (B) blue; and (C) burgundy colour morphs of *C. purpurus* from Babatngon, Leyte (yellow broken line emphasize cruciform-shaped stomach and gonads); (D) *Crambione mastigophora* from El Nido in Palawan, Philippines; (E) *Crambionella orsini* from Wasin, Kenya (Wasini Guide observations). Canal systems of a topotype in Naturalis (F; a.c.: RMNH.COEL.5027) and paratype in the MCZ (G; a.c.: MCZ IZ: CNID-1807) with coarse anastomoses = yellow dot; anastomosing canal connections with rhopalar canals = yellow arrows; actual ridges (not canals) of subumbrellar musculature due to slight specimen contraction = red arrows; interrhopalar canal = IRC; rhopalar canal = RC; rhopalium = RHO); gastrovascular canals in the burgundy (H) and blue (I) morphs of *C. purpurus* (blue and red arrows = subgenital papillae); (J) gastrovascular canals of *C. townsendi* medusa from Stiasny (1921). Photos courtesy of Wasini Guide (E) and Museum of Comparative Zoology (G).

T. Yoshida and J. Bruce observations (https://tinyurl.com/4r59543c); verified observation (*n* = 1 video) of burgundy blubber jellyfish medusae called 'black jellyfish' and their bloom in 29 June 2023 in Bantayan Island of Cebu, myparadiseonbantayanisland9030 observations (https://tinyurl.com/yeyurtjc) (Table 1); a photo and videos (*n* = 2) of burgundy jellyfish bloom in 6 September 2023, town of Bato in Leyte, Philippines, anonymous personal communication to S. R. Boco (Table 1).

Diagnosis

Catostylidae possessing oral arms lacking terminal clubs and filaments, and intracircular network of anastomosing canals connected with both rhopaliar and interrhopaliar radial canals, differing from the congeners on the absence of any ornamentation on the exumbrella (ridges, granules, striations).

Description

Holotype: bell with uniform dark brownish to purple colouration in life; bell diameter 115 mm, and height 35 mm; oral arms 58 mm long with smooth proximal section: 7 mm in length and, lower distal portion: 51 mm long (A. G. Mayer in 1910). New specimens typical of *Catostylus*, with bell diameter ranging from 28.9–42 mm (juvenile) to 52.4–125 mm (mature). Bell hemispherical and slightly flattens after preservation in 4% formalin, exposing the oral arms (Figures 1C and 2A–C). Exumbrella smooth (Figure 2A–C; as in Figure 2D, E) and are
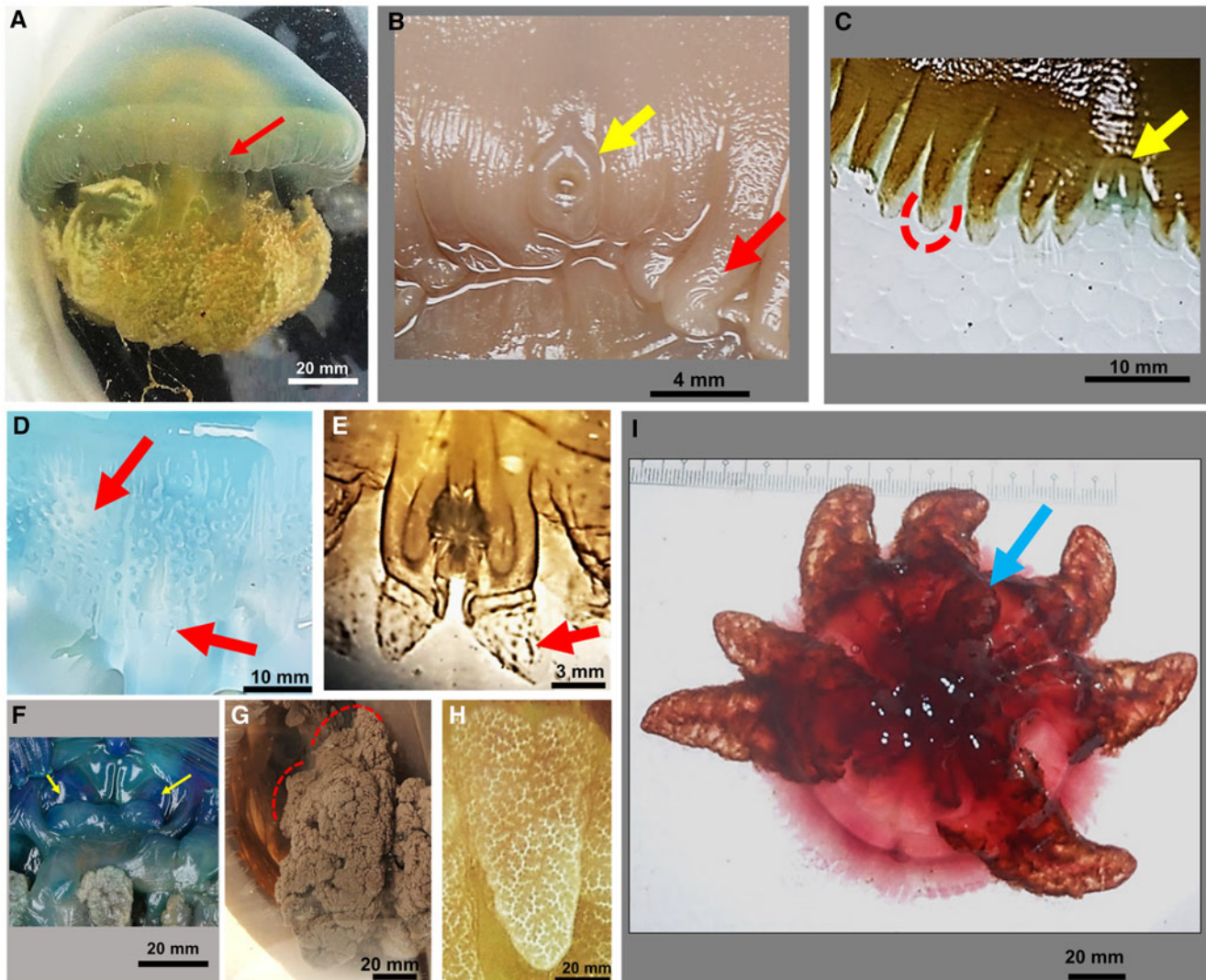
Figure 3. Morphology of *C. purpurus*: (A) *C. purpurus* medusa collected from Biliran, central Philippines (museum accession code, a.c.: NMP2017C-06, Table 1) with silver-like spot (statocyst) in the rhopalium (red arrow); (B) section of bell margin of the topotype (RMNH.COEL.5027) with microscopic spots on the rhopalium (yellow arrow) and lappets (red arrow); (C) marginal lappets of burgundy *C. purpurus* from Babatngon, Leyte (a.c.: NMP2017C-08; yellow arrow = rhopalium; red broken line emphasizes shape of the lappet tip); (D) umbrella margin and lappets (arrows) of *C. perezi* medusa; (E) rhopalium with lappets (red arrow) of *C. purpurus* (NMP2017C-08); (F) subgenital ostium (yellow arrows = edges) and oral arms (G) of a *C. purpurus* topotype specimen (RMNH.COEL.5027; red broken lines = convex-shaped 'top' end of oral arms on the subumbrella); (H) oral arm of a living *C. purpurus* specimen (a.c.: NMP2017C-08); (I) subumbrellar view of a burgundy colour morph, with one small oral arm (blue arrow), from Catbalogan, Samar (a.c.: UPDIM-Cni-Scy-013-001).

unlike the medusae of *Catostylus ouwensi*, *C. mosaicus*, and *C. tagi* with striated to coarsely granulated surface and lappets with ridges (Figure 1D, G) and *C. townsendi* with dark to greenish constellation-like spots (Figure 1E). Cruciform-shaped gonads and stomach are slightly visible from translucent exumbrella (Figure 2B, C). Gastric canal system has eight rhopaliar and eight interrhopaliar canals. Intracircular anastomosing canal network connects to rhopaliar and inter-rhopaliar canals, typical of *Catostylus* (Figure 2F–I). Intracircular anastomoses are coarse compared to fine-meshed marginal anastomoses of the canal system (Figure 2F–I), but unlike the canal system of *C. townsendi* with slightly coarser intracircular anastomoses (Figure 2J). Subgenital papillae, 3–4 per individual, with average width of 4.7 and 6.21 mm length, are positioned parallel to rhopaliar canals and in front of subgenital ostia (Figure 2H, I); 4–5 (among juveniles) and 5–11 (mature) marginal lappets per octant. Thin transparent to translucent membrane connects marginal lappets (Figure 3A–C; E). Marginal lappets have microscopic spots visible at a stereomicroscope's 40× total magnification with leaf-tip- to dome-shaped tips (Figure 3A–C; E). Lappets are smooth macroscopically (Figure 3A–C) unlike

those of *C. mosaicus* with macroscopic striations, Arabian *C. perezi* with minute warts (Figure 3D), *C. townsendi* with fine granules, and *C. ouwensi* with fine striations. Silver-like dots (statocyst) in rhopalia as in original descriptions of paratypes (Figure 3A). Rhopalia are positioned inside a 'pit' between paired rhopaliar (ocular) lappets, distinctively smaller than adjacent velar lappets (Figure 3A–C). Smooth subgenital ostia (Figure 3F), 4 per individual, with average width of 13.1 mm. Three-winged oral-arms, eight per individual (Figure 3G–I), with average lengths of 19.5 mm (juveniles) and 34.3 mm (mature). Oral arms without appendages (Figures 1C and 3G–I).

Remarks

Catostylus purpurus medusae in this study resemble *C. townsendi*. This observation conforms to Light (1921) that mentioned this similarity. The smooth bell texture of the jellyfish here looks like the umbrella of *C. perezi* (Figure 1E), *Crambione mastigophora* (Figure 2D), and *Crambionella orsini* (Figure 2E), but *C. orsini* medusa has prominent ridges on marginal lappets (Figure 2E). *Catostylus* here has oral arms with no appendages

unlike other Catostylidae jellyfish like *C. mastigophora* with string-like filaments (Figure 2D) and *C. orsini* with leaf-tip-shaped terminal appendages (Figure 2E). However, the Philippine blubber jellyfish's gastrovascular canal system and morphological features, such as bell shape, texture, and lack of colour spots or bands, affirm its classification as *C. purpurus*, distinct from *Acromitoides* species and other Western Pacific species of *Catostylus*: *C. townsendi*, *C. ouwensi*, and *C. mosaicus*. Moreover, Stiasny (1921) deemed Mayer's (1910, 1915) and Light's (1914, 1921) descriptions insufficient and proposed the new genus to accommodate the taxon under the binomen *A. purpureus*. This taxon's spelling remained in Stiasny (1924*b*: 39–45, 1926: 246) until Kramp (1961) started to use the original epithet *purpurus* again. Regardless of these historical contexts, our new findings on the morphology including re-examination of type specimens of the Philippine jellyfish validate the species as a member of the genus *Catostylus*, i.e. as *C. purpurus*.

We found *C. purpurus* shares some similarities with *Acromitoides stiphropterus* (Stiasny, 1921; see also systematics in Table S2 and Figure S2, Supplementary materials), one of the two species under genus *Acromitoides* aside from *A. purpurus* (now a synonym in *Catostylus*). Notably, *A. stiphropterus* has a hemispherical bell with smooth exumbrella. However, this jellyfish has brown spots that fade near the bell margin similar to *C. townsendi*, but unlike *C. purpurus*. The gastric canal system of *A. stiphropterus* contains wide-meshed intracircular anastomoses solely connected to inter-rhopaliar (adradial) canals, a feature that deviates from the form in *Catostylus* spp. (Stiasny, 1921). Schultze (1897) originally described this jellyfish (as *Crambessa stiphroptera*) using one preserved specimen with damage such as the prominent abrasion on coronal (ring) muscles, but he did not provide a preserved specimen for future examination (Table S2 and Figure S2, Supplementary materials). The presence or absence of a subgenital papilla, a diagnostic feature of a Catostylidae genus, in this jellyfish was also not described (Schultze, 1897; Stiasny, 1921). Without sufficient morphological descriptions maintaining the validity of *A. stiphropterus* and the morphology of this jellyfish leaning to many features of *C. townsendi*, *A. stiphropterus* will remain a *species inquirenda* until at least morphological features from a series of specimens without damage, will show whether the species is new or belongs to a rhizostome family like Catostylidae. Since no stable sets of morphological traits (e.g. shape of subumbrellar papillae) support the genus *Acromitoides*, this genus requires further taxonomic investigation. Thus, we establish *Acromitoides* as *genus inquirenda* in this study.

Etymology

Mayer (1910, 1915) did not specify the origin of the name *purpurus* after establishing this species. The term 'purpurus' may be a variant of the Latin word 'purpureus', which means 'purple' (e.g. *Leptolalax purpurus*). *Purpureus* may be used to describe some purple characteristic of a species like *Cenchrus purpureus* with sometimes purple, foxtail-shaped flower. *Purpurus* here may refer to the brown, purple, and burgundy colour morphs of the medusae found in Manila Bay.

Local names

Names are *salabay* and *dikya* (Tagalog in Cavite and Bataan, northern Philippines); *budol*, *bokya*, *bukya* (Waray in Leyte and Biliran, eastern Philippines); *bokya* (Cebuano); and *bulbog* (Cebuano in Ormoc, Leyte and Lanao del Norte, southern Philippines). However, *salabay* may refer to chirodropid box jellyfishes and other species with prominently trailing tentacles like the compass jellyfish, *Chrysaora* spp., in Tagalog and Cebuano languages. Here, we also establish English common names such as 'Philippine blubber jellyfish' and 'burgundy blubber jellyfish' when writing about this species since these terms specifically refer to this jellyfish with brown to burgundy-coloured medusae and other colour morphs such as white and blue morphs.

Molecular analysis

The Philippine *C. purpurus* medusae exhibit close *p*-distances of 0.000–0.014 (*cox1*) and 0.00–0.00 (16S). *C. townsendi*, found in southeast Asian waters, shows a genetic distance of 0.161–0.166 to *C. purpurus* in *cox1* and 0.0628 in 16S (Table 2). Similarly, *C. purpurus* differs genetically from *C. mosaicus* from Australia (0.171 in *cox1* and 0.063 in 16S) (Table 2).

Our phylogenetic analyses show *C. purpurus* specimens form a clade with 100% bootstrap support (*cox1*; 16S), separated genetically from *C. townsendi* and the Australian blubber jellyfish, *C. mosaicus* (Figure 4). Analyses of both markers unite the species of *Catostylus* into a single clade (bootstrap indices of 81 and 97 for *cox1* and 16S), but differ in the specific relationships among the three species. Bootstrap support for the topology based on the *cox1* dataset is poor, while the 16S data provide moderate support (bootstrap index = 73) for *C. townsendi* as the sister species of *C. purpurus* (Figure 4). Further analyses using phylogenetic trees based on all available sequences of *Catostylus* for both genes reveal that Western Pacific species (*C. purpurus*, *C. townsendi*, *C. mosaicus*) form a distinct clade with high support (94% for *cox1*, 98% for 16S), separate from non-Western Pacific species (*Catostylus* sp. 1 in Central America, *C. tagi* in Portugal; see Figures S3 and S4, Supplementary materials). In the *cox1* tree, *C. townsendi* forms a clade, and another clade includes *Catostylus* sp. 2 and *C. purpurus*, both with 100% bootstrap indices (Figure S3, Supplementary materials). The 16S topology shows a clade of *C. townsendi* with high support (index = 93%) and another clade uniting *C. mosaicus* and *C. purpurus* with 98% support index (Figure S4, Supplementary materials).

Ecology

Catostylus purpurus medusae exist in many ecoregions of the Philippines (Figure 1A) including the West Philippine Sea region (i.e. Cavite and Bataan provinces surrounding Manila Bay), Visayan region (i.e. Cebu, Leyte, Biliran, Samar, and Lanao del Norte provinces) and Southern Philippine Sea with Marabut town in Samar (Table 1; Figures 1B and 5A). Recent visits to the type locality (Navotas coast, Metro Manila; coordinates: 14° 40′08.3″N, 120°55′57.5″E) of *C. purpurus* from April to July and November to December 2016 did not reveal the jellyfish in the area due to unknown causes.

Blooms of this jellyfish appear in several coastal waters in the Philippines, particularly in Pasay coast, Metro Manila (14° 31′55.8″N, 120°58′41.5″E), Orion town, Bataan (14°35′06.2″N, 120°35′29.2″E), towns of Carigara (11°18′16.2″N, 124° 40′52.3″E) and Bato (10°19′36.93″N, 124°47′12.56″E) in Leyte, and Panguil Bay (8°06′56.0″N, 123°51′49.6″E) in northern Mindanao (Figure 5A–D). These blooms are distinguishable from those of *C. townsendi* with prominent colour spots on the central exumbrella to the lappets, like those that occur in Palawan, Philippines and northern Thailand (Figure 5A; E, F; Table S1, Supplementary materials). Unlike the medusae of Philippine *Catostylus*, *C. mosaicus* has a distinct granulated exumbrella, visible among blooms observed in Australia (Figure 5G).

Besides the burgundy morphs of *C. purpurus*, the species also occurs as other colour morphs, like blue morphs in central Philippines (Cebu, Leyte, and Samar regions), and northern

Table 2. Uncorrected pairwise distances for cytochrome oxidase I (*cox1*) and ribosomal RNA gene (16S) between *C. purpurus* and other scyphozoan jellyfish species, e.g. *C. townsendi* and *M. papua*

| Species	C. purpurus	C. purpurus	C. purpurus	C. purpurus	C. mosaicus	C. townsendi	A. flagellatus
Cox1							
C. purpurus	**0.014**						
C. purpurus	**0.010**	**0.003**					
C. purpurus	**0.010**	**0.003**	**0.000**				
C. mosaicus	0.166	0.161	0.161	0.161			
C. townsendi	0.171	0.171	0.171	0.171	0.142		
A. flagellatus	0.219	0.219	0.223	0.223	0.197	0.204	
M. papua	0.240	0.242	0.242	0.242	0.239	0.234	0.253
16S							
C. purpurus	**0.000**						
C. purpurus	**0.000**	**0.000**					
C. purpurus	**0.000**	**0.000**	**0.000**				
C. mosaicus	0.092	0.092	0.092	0.092			
C. townsendi	0.063	0.063	0.063	0.063	0.096		
A. flagellatus	0.164	0.164	0.164	0.164	0.168	0.151	
M. papua	0.143	0.143	0.143	0.143	0.166	0.150	0.194

Values in bold are the lowest distances.
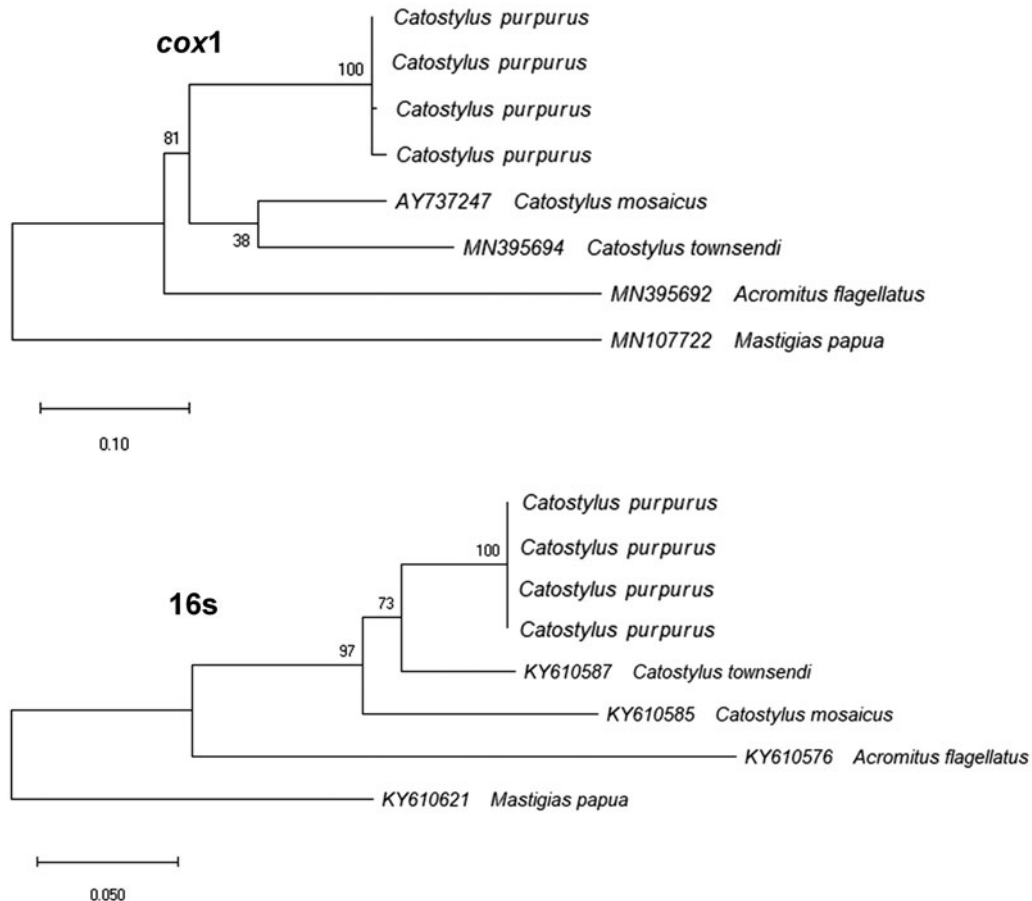
Figure 4. Phylogenetic trees based on maximum-likelihood method and Tamura–Nei models for *cox1* and 16S genes of *C. purpurus* and other scyphozoan medusae (e.g. *M. papua*). Trees are based on the highest log likelihood (*cox1*: −2210.01; 16S: 1753.65) and eight nucleotides for both genes. Numbers at nodes are bootstrap supports (%).
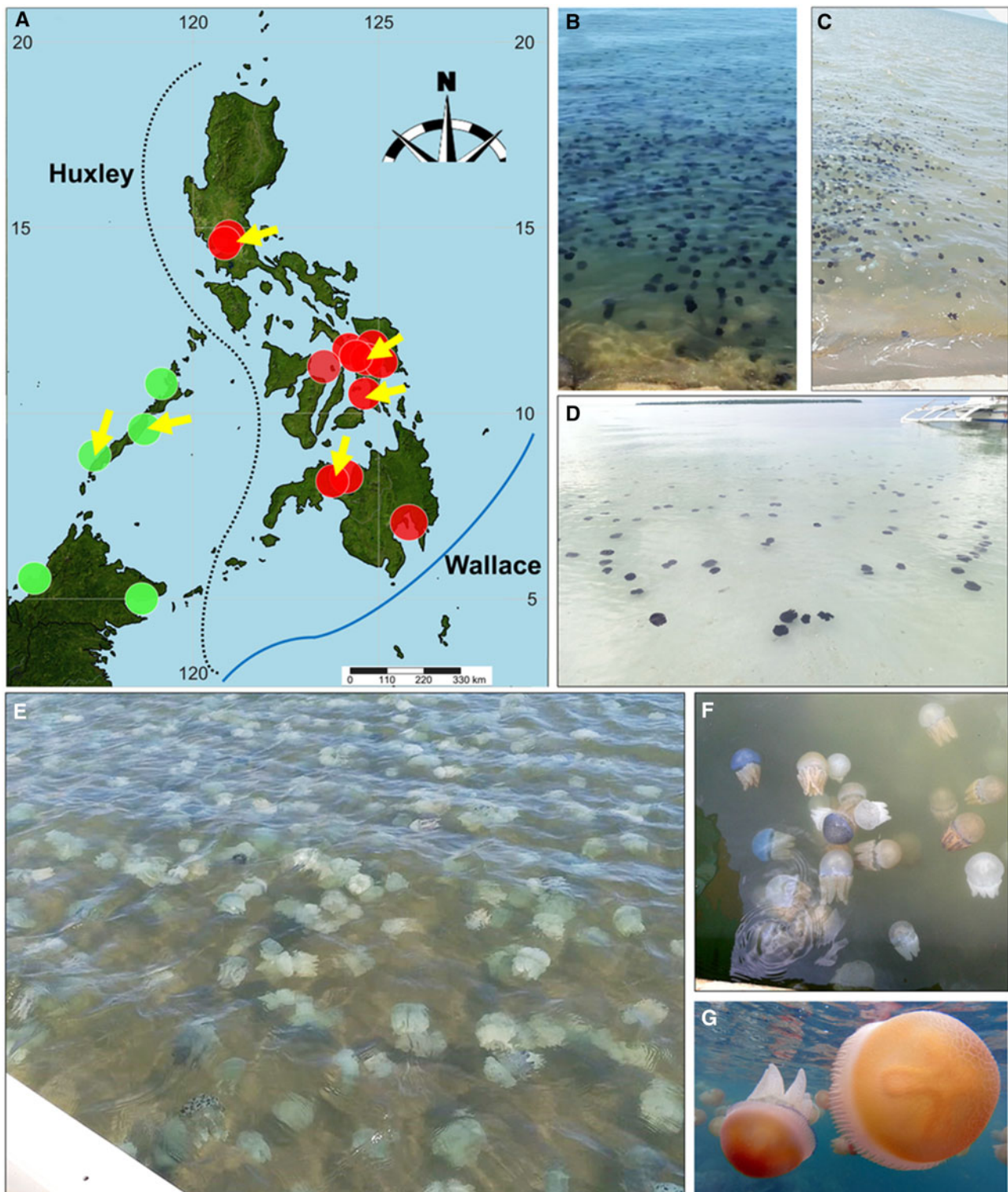
Figure 5. (A) Map of the Philippines with Huxley and Wallace boundaries, indicating locations of confirmed blooms (yellow arrows) and occurrences of *C. purpurus* (orange dots) and *C. townsendi* (green dots). Refer also to Table 1 and Table S1 (Supplementary materials) and 'Ecology' under the Results section for specific locations of these blooms; (B–D) blooms of *C. purpurus* in Orion, Bataan (B), at the coast of Carigara town (C) and Bantayan Island (D), Philippines; *C. townsendi* blooms in Narra, Palawan on February 2019 (E) and in Trat province, Thailand (F); (G) bloom of *C. mosaicus* in April 2022 in Manly coast, Sydney, Australia. Photos courtesy of A. Manlangit (B), S. Mones (C), P. Dimalaluan (E), Marine and Coastal Resources Research and Development Centre, Thailand, and K. Chanachon (F), and J. Turnbull (G).

region (Manila Bay) (Figures 2A and 5B; see also records in Table 1). Blue, orange, and white morphs exist in southern Philippines (Panguil and Iligan Bays). The medusae are abundant in warm months (April, May, and June) but also occur year-round in central Philippines (Boco *et al.*, unpublished data; see also records in Table 1).

Figures 1A, C; 2B, C; and 5A, D). In addition, thus far, medusae of *C. purpurus* associate with a number of animal ectosymbionts, including the crucifix crab *Charybdis* (*Charybdis*) *feriata*, the copepod *Paramacrochiron* sp., and juvenile carangid fish, *Alepes djedaba*.

Envenomation

Some authors (SRB, CGGC, DT) here, experienced slight burning to itchy stings upon accidental barehand handling of medusae and wading in water where the medusae occur and are abundant (>5 medusae m^{-3}) during extensive field surveys for this jellyfish in the Philippines (2013–2022). Wading in the water when *C.* *purpurus* medusae are around may cause stings even without direct contact with the medusa. This observation appears like the stings induced by cassiosomes (i.e. floating tissues with nematocysts) of some jellyfish species like *Cassiopea* spp. (Lewis-Ames *et al.*, 2020) and is consistent with Lewis-Ames *et al.*'s (2020) observation that *Catostylus mosaicus* releases similar stinging structures.

KEYS TO THE IDENTIFICATION OF *CATOSTYLUS* SPP.

The description of the texture of exumbrella and the type specimen of *Catostylus tripterus* (Haeckel, 1880) are unavailable. Further, without description of the number and arrangement of marginal lappets, subgenital papillae, circular musculature, and bell colour, the species of *Catostylus turgescens* (Schultze, 1898) is extremely doubtful. In 1921, Stiasny recognized this jellyfish as possibly regenerating or had an injury. Due to these morphological descriptions lacking diagnostic characters, we classify *C. tripterus* and *C. turgescens* as *species inquirendae* and they are absent in this key.

1	Catostylidae exumbrella with coarse granulations	2
	With completely or macroscopically smooth surface on centre of exumbrella	3
2	Exumbrellar granules fuse into rows on the marginal lappets . . . . *C. ornatellus* (Vanhöffen, 1888)	
	Without the above arrangement of granules on lappets; smooth proximal part of oral arm short, about 1/6 as long as distal three-winged part . . . . *C. mosaicus* (Quoy & Gaimard, 1824)	
3	Radial furrows prominent between centre of exumbrella and bell margin . . . . *C. cruciatus* (Lesson, 1830)	
	Absence of deep furrows on the bell	4
4	With rows of prominent rugged papillae radiating towards the margin on exumbrella . . . . 4. . . . . *C. perezi* Ranson, 1945	
	Without marginal papillae	5
5	With shallow dendritically branching furrows near umbrella margin, distal end of oral arm tapering to a point . . . . *C. tagi* (Haeckel, 1869)	
	Smooth exumbrella with fine granulations on exumbrellar margins	6
6	Exumbrella macroscopically smooth but with less prominent minute granulations . . . . 6. . . . . *C. ouwensi* Moestafa & McConnaughey, 1966	
	Entirely smooth exumbrella	7
7	Exumbrella with purple-brown, or light to dark greenish spots that usually fade at the bell margin; length of proximal part of oral arm variable, from 1/2 or 1/4 to the same length of distal three-winged part . . . . *C. townsendi* Mayer, 1915	
	Exumbrella without constellation-like colour spots	8
8	Bell slightly flattened to hemispherical, slit-shaped subgenital ostia and umbrella colour greyish-yellowish (opaque) and violet oral arms . . . . *C. viridescens* (Chun, 1896)	
	Flat to hemispherical bell with smooth exumbrella but narrow and long subgenital ostia; with microscopic spots on the lappets; with medusae of burgundy to brown, purple, blue, orange, and white colour morphs . . . . *C. purpurus* Mayer, 1910	

Discussion

Several jellyfish taxa require reassessment of their validity (e.g. in Jarms and Morandini, 2019; Gamero-Mora *et al.*, 2022). Modern methods such as integrative systematics with morphological and molecular information effectively clarify taxa of many species of jellyfish like rhizostome medusae (Gamero-Mora *et al.*, 2022; Santander *et al.*, 2022). Here, the findings support our hypothesis that the Philippine blubber jellyfish, exhibiting different colour morphs, does not belong to the genus *Acromitoides*, but rather to *Catostylus*. Thus, in this study, we rearrange the jellyfish species *A. purpurus* into the genus *Catostylus*, and confirm the validity of the species, commonly known in English as blubber jellyfish. Our integrative approach shows that *C. purpurus* can be distinguished from the other Western Pacific species of the genus, *C. townsendi* and *C. mosaicus*, with both molecular and morphological features. Hence, this study synonymizes *A. purpurus*, as a junior synonym of *C. purpurus*; against Stiasny's (1921) and Kramp's (1961) visions to keep it in a separate genus. This new arrangement with *C. purpurus* adds one to the eight valid species of the genus *Catostylus* and confirms occurrences of three *Catostylus* spp. (*C. purpurus*, *C. townsendi*, and *C. ouwensi*) in the Indo-Pacific (Figure 1A; Jarms and Morandini, 2019, 2023; Collins and Morandini, 2023). This revived Philippine taxon enhances our understanding of jellyfish biodiversity in the Indo-Pacific, a region that likely harbours additional undiscovered species of rhizostome jellyfish (Gamero-Mora *et al.*, 2022).

This study highlights the importance of examining many morphological features, including the form of the gastrovascular canal system of jellyfish, in order to garner the information necessary to diagnose scyphozoan species. The canal system, combined with

other morphological features like bell texture enabled confirmation of many other species of rhizostome jellyfish such as *C. mastigophora* and *Acromitus* spp. (Thiel, 1978; Gómez Daglio and Dawson, 2017). However, the same method of diagnosing species using canal system was used to establish *A. purpurus* (now a synonym), despite preceding evidence indicating it to be a species of *Catostylus* (in Mayer, 1910, 1915; Light, 1914, 1921). Specifically, Stiasny (1924b) mentioned that the canal system of topotypes of *C. purpurus* usually consists of anastomoses that do not connect to all rhopaliar canals. The description of these canals was based on formalin-preserved specimens (Stiasny, 1924b) and this study opposes this observation. Hence, we speculate that formalin preservation potentially induced slightly rigid musculature and contracted bell of Stiasny's (1924b) specimens. This outcome after preservation perhaps influenced the appearance of the canals and led Stiasny's (1924b) drawings of canal systems that show rhopaliar canals without connections to coarse anastomoses. The cases in Stiasny (1924a, 1931), similar to observations in Stiasny (1924b), support this speculation. Some formalin-preserved specimens of *C. mosaicus* and *Rhizostoma luteum* were examined and Stiasny (1924a, 1931) mentioned they contain canal systems that do not conform to established descriptions of the gastrovascular canal network for these two species. Stiasny (1924a, 1931) argued that these are potential 'population variations' with canal system 'anomalies' of the two species (e.g. *C. mosaicus*) without considering the possibility of error in staining the canal system due to contraction of specimens after preservation or, simply, a damage to the bell. Stiasny (1924a, 1931) might have examined malformed individuals with deformed gastrovascular canals of these species. This speculation on specimen malformation including the method of staining of canal systems warrants examination in future studies of jellyfish taxonomy. Potential damage of specimens such as predation-based injuries and effect of formalin preservation on the appearance of gastrovascular canal systems need further investigation and must be checked in a series of individuals.

Even without information on the canal system, morphological features of *C. purpurus* are shared with those of many species of *Catostylus*. Specifically, *C. purpurus* shares with *C. townsendi* and *C. mosaicus* the shape of the bell and lappets, and texture and shape of three-branched oral arms. Due to similarity of our species here to *C. townsendi*, we recommend further examination of *Catostylus* spp. using morphometric statistics. Using data of size-adjusted features of medusae will elucidate potential variation of the morphology of medusae such as the distinction of their bell shapes and texture of oral arms in future studies of *Catostylus* species (e.g. between moon jellyfish species of *Aurelia* spp.; Chiaverano et al., 2016; Lawley et al., 2021). Further, we uncovered the taxonomic status of species similar to *C. purpurus*. Through careful examination of jellyfish taxonomic literature and advances made in this study, we found that descriptions of *C. tripterus* and *C. turgescens* are incomplete, thus they are highly doubtful and not diagnostic for these species. Similarly, the status of the Catostylidae species *A. stiphropterus* will need taxonomic examination. These doubts on the taxonomy of these species have been echoed before (Mayer, 1910; Stiasny, 1921; Kitamura and Omori, 2010) and our study aligns with doubts presented in these papers. Hence, we classified *C. tripterus*, *C. turgescens*, and *A. stiphropterus* as *species inquirendae* and genus *Acromitoides* as *genus inquirenda*.

Since morphology alone may not always be sufficient to delineate species, clarifying species boundaries sometimes requires genetic analyses (Dawson and Jacobs, 2001; Dawson, 2003). Molecular approaches improved systematics understanding of rhizostomes by confirming the taxonomic lineage of Catostylidae species such as *C. mosaicus* and *Acromitus* spp. (e.g. Dawson, 2005a; Gómez Daglio and Dawson, 2017). In this study, analyses of *cox1* and *16S* sequences clearly separate *C. purpurus* from other species of *Catostylus* from the Western Pacific, i.e. *C. townsendi*, which also occurs in the Philippine region (at the western Philippine area) and *C. mosaicus* from Australia (see Figure 4). These distinct genetic profiles of *C. purpurus*, as revealed through two genetic markers, affirm its separation from other *Catostylus* species in the Western Pacific.

Regarding genetic distances, average intra-species *p*-distances (%) of 0.7 (±standard deviation) ± 0.5 (*cox1*) and 0.0 ± 0.0 (*16S*) of *C. purpurus* fall within the species-level *p*-distances measured for other rhizostome jellyfishes (e.g. *Cassiopea* sp.; Gómez Daglio and Dawson, 2017; Gamero-Mora et al., 2022). For example, *Cassiopea mayeri*, which also occurs in Western Pacific including the Philippines, exhibits 1.4–1.8% (*16S*) and 3.2–4.2% (*cox1*) within-species distances (Gamero-Mora et al., 2022). Thus, minimal genetic variation exists within the species of *C. purpurus* despite our samples that originated from different colour morphs. Meanwhile, the average % *p*-distances between *C. purpurus* and *C. townsendi* are higher (17 ± 1.2 for *cox1*) or around (6.9 ± 1.0 for *16S*) inter-clade or genus-level distances of rhizostomes such as between the species of *Mastigias* with 8.6 ± 3.2 average % *p*-distance of *cox1* in the tropical Western Pacific (de Souza and Dawson, 2018). Indeed, the *p*-distances (%) between *Cassiopea mayeri* and *Cassiopea culionensis* are lower (13.6–14.2 for *cox1*) or around (10.1–12.9 for *16S*) the average *p*-distances between *C. purpurus* and *C. townsendi*, although these upside-down jellyfishes occur in sympatry in the Philippines (see Gamero-Mora et al., 2022), unlike *C. purpurus* which exists separately by geography from *C. townsendi* to date. While the genetic differences between *C. purpurus* and *C. townsendi* support their distinction as separate species, the exact threshold for genetic distance that defines separate species remains a subject of research (Smith and Carstens, 2022). Nevertheless, the genetic evidence presented here is consistent with our morphological results. This underscores the importance of a holistic approach that integrates morphological and molecular data and employs multiple genes to support accurate species identification.

Interestingly, we find some support (through phylogenetic analysis of *16S*) that *C. purpurus* is more closely related to *C. townsendi* from the Indo-Pacific (sample from Malaysia) than it is to *C. mosaicus* from Australia. However, topology results using all available sequences of *Catostylus* showed conflicting phylogenetic relationship of *C. townsendi* to *C. purpurus*. *C. townsendi* formed a *16S* clade clearly separating this species to the Philippine *C. purpurus* (see Figure S4, Supplementary materials). The root of this inconsistency is unclear but could be linked to the unequal number of sequences between the species here. Specifically, there are fewer sequences of *C. townsendi* compared to *C. mosaicus* in the *cox1* tree, whereas in the *16S* topology, there are more samples of *C. townsendi* than *C. mosaicus* (Figures S3 and S4, Supplementary materials). While beyond the scope of our study, topologies may shift depending on the number of genetic samples available for a species or between nominated species (refer to Huang et al., 2021). Moreover, without genetic samples from all other congeners, the evolutionary trajectory of the entire genus continues to be a mystery. Nevertheless, our molecular findings mirror significant morphological differences between *C. purpurus* and other Western Pacific species such as *C. townsendi*. Notably, *C. townsendi* displays a constellation-like pattern of colour spots on the exumbrella, and *C. mosaicus* exhibits ridges or papillae on the exumbrella, both of which are absent in *C. purpurus* medusae. Despite the lack of genetic data, *C. ouwensi* from Indonesia presents a unique morphology with macroscopically visible but fine granulations on the exumbrella. These morphological differences seem to be restricted to species with relatively narrow and

distinct geographic distributions in the Western Pacific. For example, despite comprehensive surveys, we have not found *C. townsendi* coexisting with *C. purpurus*. *C. mosaicus* appears to be confined to Australia, whereas *C. ouwensi* has only been observed in Indonesia. Consequently, potential biogeographic boundaries, such as the Sulu Sea and Huxley's line, may govern the distributions of Pacific blubber jellyfish species (discussed below). These boundaries could be the isolating mechanisms that have allowed for the accumulation of distinct morphologies and genetic signatures. Thus, morphological, and molecular findings and available data of biogeographic distributions, support the species distinction of *C. purpurus*. Given this, we recommend having biogeographic information, morphology, and molecular data (as in this study) when accessible, to explain and/or assess the existence of a separate jellyfish species.

Catostylus purpurus's distribution may represent biogeographic separation of this species to other *Catostylus* species in the Western Pacific. For example, *C. purpurus* exists on the east side of Huxley's line, unlike *C. townsendi*, which occurs on the west side, particularly in western Philippines (Figure 5A). We expect this distribution pattern of this jellyfish, consistent with biogeographic gene separations observed in various marine taxa in Southeast Asia, such as the marine alga, *Gracilaria* spp. (Chasani, 2017) and squat lobster *Uroptychus naso* (Poore and Andreakis, 2011), which follow Huxley's line (Huxley, 1868). Remarkably, *C. purpurus* in the north of Wallace's line (Figure 5A) appears geographically separate from *C. mosaicus* which exists at the line's south (Australia). Although not part of this study, Wallace's line influences geographic distribution of marine species such as the reef ascidian, *Polycarpa aurata* and fiddler crab *Austruca perplexa* and we invoke this boundary as a potential factor regulating the distribution of some *Catostylus* spp. (as in Hardianto, *et al.*, 2022). If the distribution of *C. purpurus* here indeed follows these significant biogeographical boundaries (Wallace's and Huxley's), then various factors such as ocean currents, temperature profiles, and distribution of zooplankton prey, perhaps influence separation of this species from jellyfish populations in western Philippines, where *C. townsendi* occurs. Currents could also regulate transport of planulae or juvenile medusae of *C. purpurus* and could concentrate them into areas like central and central-eastern Philippines where this jellyfish exists. Therefore, we need to study the life cycle stages including the larvae of this jellyfish similar to studies on the life cycle of many *Catostylus* species, such as *C. mosaicus* and *C. tagi*, to significantly reveal the ecology and distribution of this jellyfish (Pitt, 2000; Phuangsanthia *et al.*, 2018; Gueroun *et al.*, 2021). However, these are speculations, and further research is needed to understand the exact factors controlling the distribution of Indo-Pacific *Catostylus*. Studies focusing on life cycle, habitat preferences, and potential dispersal mechanisms of this Philippine jellyfish would provide valuable insights on the occurrence of this species in the Coral Triangle.

Confirming the identity of this jellyfish taxon could benefit local communities, particularly in predicting and understanding blooms and stings by this species (as in Pitt and Purcell, 2009). Previously, misidentification has led to this species being wrongly associated with severe envenomation incidents by local communities and news outlets in Cebu, central Philippines (Cordova, 2023; Madarang, 2023). However, unlike other species, jellyfishes of the Catostylidae family, such as *C. purpurus*, do not appear to cause extreme envenomation such as Irukandji-like stings or fatalities (Williamson *et al.*, 1996; Peach and Pitt, 2005; this study). Instead, they can induce 'stinging water' like upside-down jellyfishes, *Cassiopea* spp. (Lewis-Ames *et al.*, 2020). Further, confirming the presence of this species can potentially aid predictions of the frequency and magnitude of blooms of this jellyfish, since

understanding this species means we know they can form large aggregates (e.g. thousands of medusae) of jellyfish during a bloom. This is unlike other blooms such as those of the cubozoan, *Carybdea* spp., or other scyphomedusae like *Chrysaora chinensis* whose occurrences are sporadic (Kingsford and Mooney, 2014; Syazwan *et al.*, 2021; Terenzini *et al.*, 2023). The blooms of *C. purpurus* could influence biogeochemical cycles in an area, affecting the ecosystem's carbon and nutrient flow (*sensu* Wright *et al.*, 2021). But, predicting the magnitude of blooms of this jellyfish species and their influence on geochemical cycles will require examination beyond taxonomy such as future ecological studies of *C. purpurus*. Considering the potential influence of jellyfish blooms such as those of this Philippine jellyfish, on ecosystems and human activities, we need to understand ecological maintenance of populations of this species, a task that can be effectively initiated through accurate taxonomic identification of the species – highlighting the importance of zoological studies and systematics surveys.

Conclusion

Our study provides compelling evidence that the burgundy blubber jellyfish found in the Philippines belongs to the species *C. purpurus* Mayer, 1910, previously named as *A. purpurus*. Medusae of *C. purpurus* are taxonomically separate from related *C. townsendi* and *C. mosaicus*, based on combined genetic and morphological findings. Morphological differences between *C. ouwensi* of Indonesia and this Philippine species were significant to classify *C. purpurus* as a species separate to the other Western Pacific species, *C. ouwensi*. Validating this *Catostylus* species contributes to our understanding of jellyfish biodiversity in the Indo-Pacific region, particularly in the marine species-rich region of the Philippines. Our study also enabled revision of several taxa into *species inquirendae* (*C. tripterus*, *C. turgescens*, and *A. stiphropterus*) and a *genus inquirenda* (*Acromitoides*). This study highlights the need for further research into the occurrences, distribution, and ecology of scyphozoan jellyfishes in the Indo-Pacific.

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