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Redescription of the enigmatic jellyfish, *Crambionella annandalei* (Cnidaria: Scyphozoa) from Indian waters

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Abstract

The catostylid jellyfish, *Crambionella annandalei* was originally described by Rao (1932) based on a preserved specimen collected from the Andaman Sea. Since then, no detailed taxonomic studies have been conducted and the species is often misidentified. Here, we provide a detailed morphological re-description of *C. annandalei* from fresh material collected at a variety of locations along the east coast of India. The species can be distinguished from its congeners by a combination of morphological characters, the most important of which are the proportion of terminal club length to oral arm length (0.48 ± 0.031), the proportion of the distal portion of the oral arm to naked proximal portion (7.25 ± 0.268) and the body colour. The occurrence of intra-specific colour variation in fresh specimens was also observed in the present study.

Introduction

The family Catostylidae comprises six genera and 23 species (Collins *et al*., 2020). The genus *Crambionella* was first described by Stiasny (1921) and is characterized by the presence of three-winged, stout and pyramidal oral arms lacking whip-like filaments but with terminal clubs (Stiasny, 1921; Rao, 1931). Medusae also possess an intra-circular network of anastomosing canals that communicates with the ring canal but not the stomach, and occasionally with adjacent radial canals (Stiasny, 1922; Kramp, 1961). Lappets are divided by a deep furrow and are free of any anastomosing canals (Stiasny, 1922, 1937; Rao, 1931).

The genus comprises four species, viz. *Crambionella orsini* (Vanhoffen, 1888), *Crambionella stuhlmanni* (Chun, 1896), *Crambionella helmbiru* Nishikawa, Mulyadi & Ohtsuka, 2014 and *Crambionella annandalei* Rao, 1931 (Collins *et al*., 2020). Although these four species have distinct, if overlapping distributions in coastal waters, our knowledge about them differs greatly. *Crambionella orsini* is the type species for the genus and has been widely reported from the northern Indian Ocean: from Assab, Red Sea (Vanhoffen, 1888); off Madras (Menon, 1930); around Krusadai Island, Gulf of Mannar (Menon, 1936); in the Gulf of Oman and in the Straits of Hormuz (Stiasny, 1937; Billett *et al*., 2006; Daryanabard & Dawson, 2008) as well as the Iranian Gulf (Kramp, 1956); off Pondicherry and Travancore along the east (Ranson, 1945) and west (Nair, 1946) coasts of India, respectively. *Crambionella stuhlmanni* was originally described from material collected around Zanzibar (Chun, 1896), but has also been recorded from Mozambique (Stiasny, 1922) and Madagascar (Ranson, 1945), and from the east coast of South Africa (Neethling *et al*., 2011; Perissinotto *et al*., 2013). *Crambionella helmbiru* is a recently recognized species from Cilacap and Karang Duwur, central Java, Indonesia (Nishikawa *et al*., 2009; Kitamura & Omori, 2010; Nishikawa *et al*., 2014).

Crambionella annandalei was originally collected from the Andaman Sea near Port Blair by Annandale and Prashad in 1923, and kept in the Museum of the Zoological Survey of India, only to be formally described in 1931 by Rao (1931). In that paper, Rao (1931) mentioned that the species could also be found along the coasts of Puri (Odisha), Vizagapatam (Andhra Pradesh) and Madras (Tamil Nadu). It has subsequently been recovered from the mouth of the Kalatan River, Myanmar (Kitamura & Omori, 2010) and the Digha coast, west Bengal (Sarkar *et al*., 2002). Whilst Menon (1930) identified what he thought at the time was *C. stuhlmanni* from the Madras coast, this has subsequently been regarded as *C. annandalei* (Kramp, 1961).

Our knowledge of the diversity of Scyphozoa is changing, as we come to understand that cryptic speciation in the group is relatively common and that the descriptions on which species definitions are based are incomplete (e.g. Ras *et al*., 2020). Here, we provide a detailed taxonomic re-description of the *Crambionella annandalei* from the Western Bay of Bengal.

Fig. 1. *Crambionella annandalei* Rao (1931) from Molapeta landing centre, Kakinada.

Materials and methods

Specimens (Figure 1) were collected from various locations around India: 40 specimens from gillnet landings along the coast of Andhra Pradesh between March and July 2018; two specimens from trawl by-catch at Astaranga Fishing Harbour, Puri, Odisha coast on 23 March 2019 and two specimens from gillnet landings at Gulf of Mannar, Mandapam, Tamil Nadu coast on 15 July 2018 (Figure 2). The specimens were brought to the laboratory and photographed, and the umbrella diameter (mm) and wet weight (g) individually determined. A total of 33 morphological features were measured from the fresh specimens using digital Vernier callipers (Table 1 & Figure 3A–F), following Neethling *et al.* (2011) and Nishikawa *et al.* (2014). The canal systems were injected with Rose Bengal to highlight their arrangement, after which specimens were preserved in 10% formalin.

As the size of individuals change, the measures on morphological features may also change, which makes it difficult to compare the morphological features between individuals. Therefore, all the morphometric variables were converted into proportions relative to external bell diameter (BD) for size independent comparison (Table 2). In order to compare the multivariate morphology of the specimens collected here with that of *Crambionella stuhlmanni* and *Crambionella orsini*, a Canonical Analysis of Principal Coordinates (CAP) routine was executed in PRIMER-7, using comparable data provided by MJ Gibbons (see Neethling *et al.*, 2011). Standardized data were first correlated against BD for each species and those features that remained size-dependent were removed. Data were then normalized and a resemblance matrix based on Euclidean distance was constructed between all specimens. Following Anderson *et al.* (2008), we used the 'leave one out' routine to determine the subset of PCO axes to be used in the CAP (e.g. Ras *et al.*, 2020). It was not possible to include *Crambionella helmbiru* in this analysis owing to a lack of data.

Results

SYSTEMATICS

Order DISCOMEDUSAE Haeckel, 1880
Suborder DAKTYLIOPHORAE Stiasny, 1920
Family CATOSTYLIDAE Gegenbaur, 1857
Genus *CRAMBIONELLA* Stiasny, 1921
Crambionella annandalei Rao, 1931
(Figures 1 & 3–7; Tables 1–3)

Crambionella annandalei: ZMIP.492/1, Zoological Survey of India (Indian Museum), bell diameter: 170 mm, locality: Andaman Island, Port Blair, December, 1923, Annandale and Prashad, p. 50–55, figs 4–8, pls III, IV, fig. 1; Kitamura & Omori, 2010, fig. 4, pp. 109–110; Sarkar *et al.*, 2002, pp. 31–33.

Crambionella stuhlmanni: Menon M.G.K. (1930), Bulletin of Madras Government Museum (N.S), III (I), p. 18, pl. III, figs 14 a, c & e.

MATERIALS EXAMINED

Forty specimens (bell diameter: 65–310 mm and weight: 13.6–1500 g), March to July, 2018, Pudimadaka, Rajanagaram, Molapeta, Bangarammapalem, Manginapudi (08°20 03.54N 77°

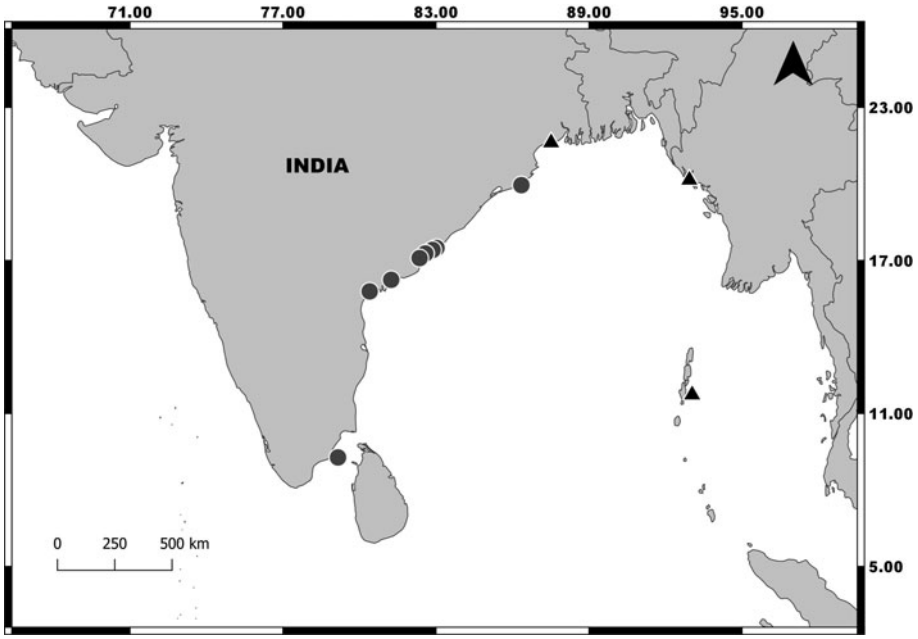

Fig. 2. Distribution pattern of *Crambionella annandalei* in the Indian Ocean (triangle: reported from Andaman Island, Myanmar and West Bengal; circle: occurrence in the present study along the east coast of India).

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Table 1. Morphological measurements of *C. annandalei* from Andhra Pradesh

Morphological feature number	Morphological feature description (mm)	Range	Mean ± SE
1	External umbrella diameter to tip of lappets	65.00–310.00	186.5 ± 18.2
2	External umbrella diameter to base of lappets	43.33–250.00	136.8 ± 14.2
3	Umbrella height	12.00–75.00	39.4 ± 4
4	Width of oral arm base	02.00–14.33	7.3 ± 0.8
5	Length of the oral arm	43.33–228.80	115.7 ± 11.8
6	Length of proximal portion (naked portion) of the oral arm	05.42–25.00	13..9 ± 1.3
7	Length of distal portion (trifoliate winged and terminal club) of the oral arm	37.68–208.80	101.9 ± 10.7
8	Depth of oral arm (including naked and ventral trifoliate winged portion)	06.50–30.00	18.1 ± 1.8
9	Depth of naked portion of oral arm	02.60–22.00	11.1 ± 1.4
10	Depth of trifoliate winged portion of oral arm	05.42–26.00	16.3 ± 1.6
11	Length of terminal clubs of oral arms (abaxials)	13.20–174.60	65.3 ± 9.6
12	Length of terminal clubs of oral arms (adaxials)	16.25–144.60	54.6 ± 7.5
13	Width of terminal clubs of oral arms	04.33–25.00	13.5 ± 1.5
14	Oral disc diameter	18.57–125.00	60.1 ± 6.9
15	Inter-ostia width	11.80–55.00	33.2 ± 3.2
16	Width of ostia	04.33–25.00	11.6 ± 1.5
17	Length of ostia	05.42–30.00	17.7 ± 1.8
18	Internal umbrella diameter to tip of lappets	52.82–270.00	151.2 ± 14.9
19	Internal umbrella diameter to base of lappets	33.33–201.00	108.8 ± 10.6
20	Ring canal diameter	38.69–190.00	101.4 ± 10.3
21	Gonadal diameter along per-radial axis	50.00–103.00	90.2 ± 4.3
22	Gonadal diameter along ad-radial axis	40.00–90.00	71.6 ± 3.8
23	Number of velar lappets in each octant	14	14
24	Number of pointed conical tubercles on velar lappets	13–19	13–19
25	Number of rhopalia	8	8
26	Number of rhopaliar canals	8	8
27	Point of termination of rhopaliar canals	Tip of lappets	
28	Number of inter rhopaliar canals	8	8
29	Point of termination of inter-rhopaliar canals	Ring canal	–
30	Number of anastomoses connecting with the ring canal	4–12	–
31	Number of primary folds in each section of gonads	5–30	–
32	Number of annular muscles	65	65
33	Number of ostia	4	4
34	Weight (g)	13.60–1500.00	524.8 ± 89

58 24.48E), coll. P. R. Behera, depth 7–50 m, gear: gillnet; two specimens (bell diameter: 120–125 mm and weight: 450–460 g), 23 March 2019, Astaranga Fishing Harbour, Puri, Odisha coast (19°58′27.102″N 86°20′20.9544″E), coll. S.K. Roul, depth: 30–40 m; gear: multiday bottom trawl; two specimens (bell diameter: 150–160 mm and weight: 500–550 g), 15 July 2018, Gulf of Mannar, Mandapam, Tamil Nadu (9°16′21.85″N 79° 08′13.88″E), coll. R. Saravanan, depth 5–10 m, gear: gillnet.

Eight specimens collected by P.R. Behera from the Pudimadaka landing centre were deposited in the Designated National Repository (DNR) of ICAR-CMFRI with accession numbers CA 3.1.1.1–CA 3.1.1.8. Two specimens collected from the Gulf of Mannar, Tamil Nadu were deposited in the Marine Biodiversity Museum of Regional Centre of ICAR-CMFRI, Mandapam with accession numbers MMM-CMFRI 18001 and MMM-CMFRI 18002.

Description. Umbrella hemispherical in shape, diameter 65–310 mm, thickened centrally, thinning to margin (Figure 4). Exumbrella surface smooth, finely granulated apically. Colour in life, variable: exumbrella of six specimens cream, with single reddish brown spot on each velar lappet (Figure 5A); 10 uniformly cream (Figure 5B); balance either light brown (Figure 5C) or light yellow (Figure 5D); light brown in colour on preservation.

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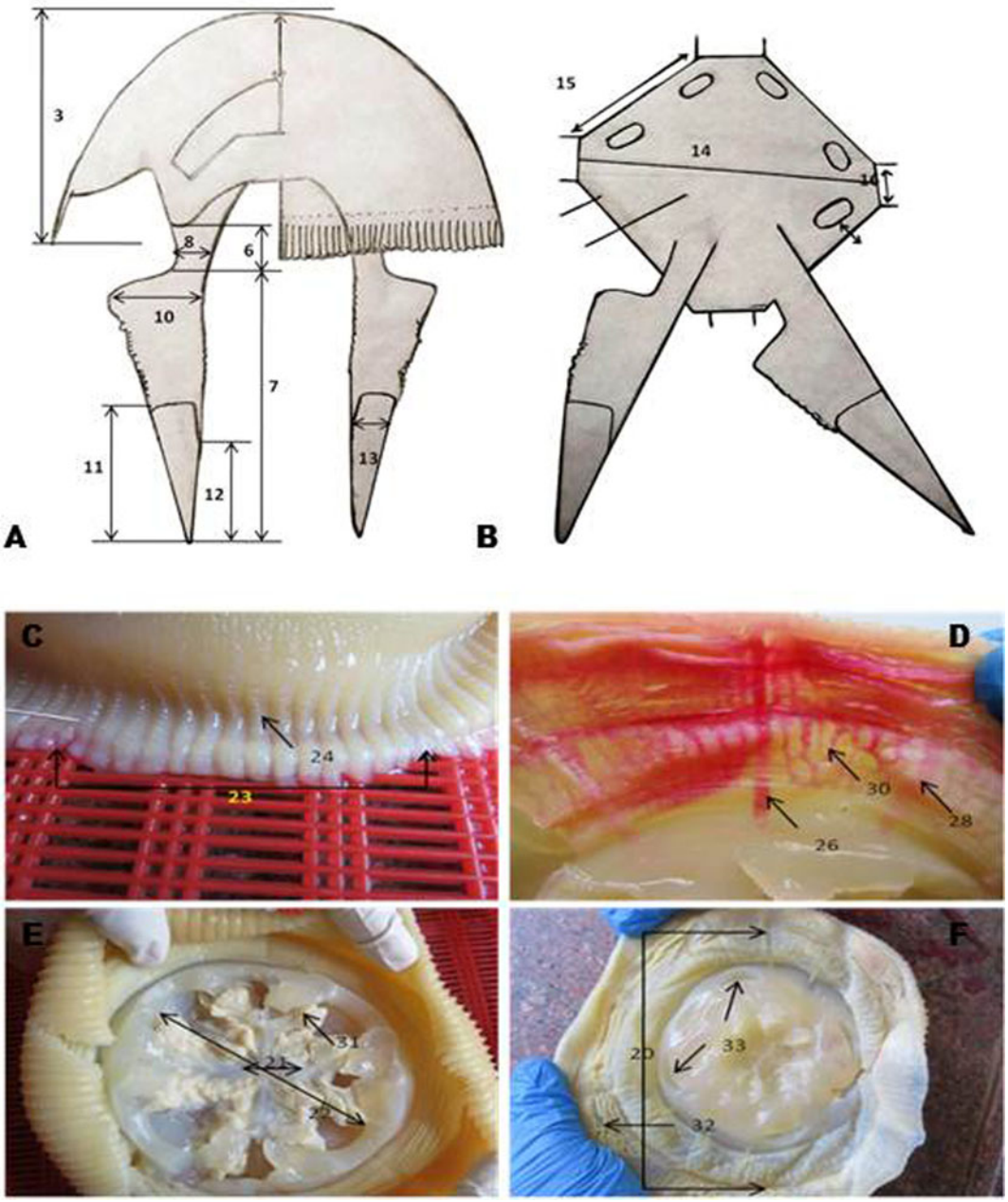

Fig. 3. Morphological features measured on *Crambionella annandalei* collected from the east coast of India. (A) Schematic diagram of a longitudinal section along per-radial axis of a specimen (adapted from Neethling *et al*., 2011); (B) schematic diagram of the oral disc, from a subumbrella view (adapted from Neethling *et al*., 2011); photograph showing the exumbrella view (C) and subumbrella view (E & F) of *C. annandalei* demonstrating various morphological measurements; subumbrella view showing the intra-circular anastomosing canal networks, after injecting Rose Bengal solution (D). Only two of the eight oral arms are shown in A and B; for details see Table 1.

Umbrella margin lacking tentacles, divided into 14 narrow velar lappets per octant, separated by deep furrows and bearing a single row of (13–19) pointed tubercles along the length of their mid-line on a prominent ridge: tubercles vary in size, largest proximally and smallest at bell margin (Figure 6A). With eight rhopalia situated equidistantly around bell margin, set in deep notches; each with a short, stout stalk with a spherical mass at its free end enclosed in a membrane; flanked by a pair of small, narrow and elongated rhopaliar lappets that diverge distally and do not extend beyond the velar lappets (Figure 6B).

Eight oral arms arise in pairs from the oral disc of the subumbrella. Each oral arm is divided into a naked proximal portion, cylindrical in cross section and without frills (ratio to bell diameter: 0.07) and a distal, three-winged portion supporting foliaceous appendages amongst mouthlets (more numerous on adaxial sides) (Figure 6C) and with terminal club (ratio to bell diameter: 0.55). Terminal clubs long, stout, tapering distally, terminated with pointed tips without mouth frills or appendages, longer abaxially than adaxially (Figures 4 & 3A).

Oral disc octagonal (centre cross-shaped), diameter less than half of the external bell diameter (Table 1). Four genital ostia present, crescent-shaped, elevated and thickened along the edge. Ostia and inter-ostia width not equal. Gonads rounded in shape, cream in colour; observed in specimens >110 mm bell diameter (Figure 3E). Subumbrella with 65 well-developed annular muscles, interrupted into two distinct regions by a groove along the ring canal. The outer is wide and has well defined 'curtain-like' muscles and the inner is narrow, and its muscles are comparatively less conspicuous.

With 16 radial canals, eight rhopaliar (four per-radial and four ad-radial) and eight inter-rhopaliar (inter-radial); rhopaliar

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Table 2. Standardized morphological features of *C. annandalei* from Andhra Pradesh

Morphological feature (mm)	Mean	SD	N
Umbrella height	0.21	0.11	44
Width of oral arm base	0.04	0.02	44
Length of proximal portion (naked portion) of the oral arm	0.07	0.04	44
Length of distal portion (trifoliate winged and terminal club) of the oral arm	0.55	0.30	44
Depth of oral arm (including naked and ventral winged portion)	0.10	0.05	44
Depth of naked portion of oral arm	0.06	0.04	44
Depth of trifoliate winged portion of oral arm	0.09	0.05	44
Length of terminal clubs of oral arms (abaxials)	0.35	0.27	44
Length of terminal clubs of oral arms (adaxials)	0.29	0.18	44
Width of terminal clubs of oral arms	0.07	0.04	44
Oral disc diameter	0.33	0.20	44
Inter-ostia width	0.18	0.09	44
Width of ostia	0.06	0.04	44
Length of ostia	0.10	0.05	44
Internal umbrella diameter to tip of lappets	0.81	0.42	44
Internal umbrella diameter to base of lappets	0.58	0.30	44
Ring canal diameter	0.54	0.29	44
Gonadal diameter along per-radial axis	0.48	0.12	44
Gonadal diameter along ad-radial axis	0.38	0.11	44
Number of velar lappets in octant	14	0.00	44
Number of pointed conical tubercles on velar lappets	15	00	44
Number of rhopalia	8	00	44
Number of rhopaliar canals	8	00	44
Number of inter-rhopaliar canals	8	00	44
Number of anastomoses connecting with the ring canal	7.25	1.35	44
Number of primary folds in each section of gonads	18.45	4.28	44
Number of annular muscles	65	00	44
Number of ostia	4	00	44
Umbrella height: External umbrella diameter to tip of lappets	0.21	0.02	44
Length of distal portion of the oral arm: Length of proximal portion of oral arm	7.25	1.42	44
Oral disc diameter: External umbrella diameter to tip of lappets	0.32	0.08	44
Width of ostia: Inter ostia width	0.36	0.13	44
Length of ostia: width of ostia	1.50	0.65	44
Length of terminal clubs of oral arm: Oral arm length	0.48	0.17	44
Oral arm length: External umbrella diameter to tip of lappets	0.63	0.10	44

canals extend to umbrella margin, inter-rhopaliar canals end at the ring canal (Figure 6D). Intra-circular anastomosing network extends over less than half the area between radial canals and connects to the ring canal only (Figure 3D); rhopaliar lappets each with a short, blind extension of the rhopaliar canal (Figure 6C). Eight canals extend from the central gastric cavity down the middle of the oral arms; axial canal in terminal club giving rise to narrow transverse canals penetrating into each wing (Figure 6D).

Discussion

The CAP plot is shown in Figure 7, and is based on the following standardized features: umbrella height, depth of winged portion of oral arm, length of terminal clubs of oral arm (adaxials), oral disc diameter, width of ostia and length of ostia and the ratio between length of ostia: width of ostia. All other features were correlated with specimen size and were excluded. The plot shows a clear separation of the three species using two CAP axes; the canonical correlation associated with the first is high ($\delta_1^2 = 0.92$, $\delta_2^2 = 0.17$). Using the 'leave-one-out' procedure, four orthonormal PCO axes were used in the final CAP analysis, and 94.5% of all specimens were correctly assigned to the correct a priori taxon (two specimens each of *C. annandalei* and *C. stuhlmanni* were misidentified as *C. orsini*).

A character matrix highlighting the morphological features that differ among the four *Crambionella* species and the *Crambionella* material described here is given in Table 3. Whilst it is clear that there is overlap in some measures and meristics,

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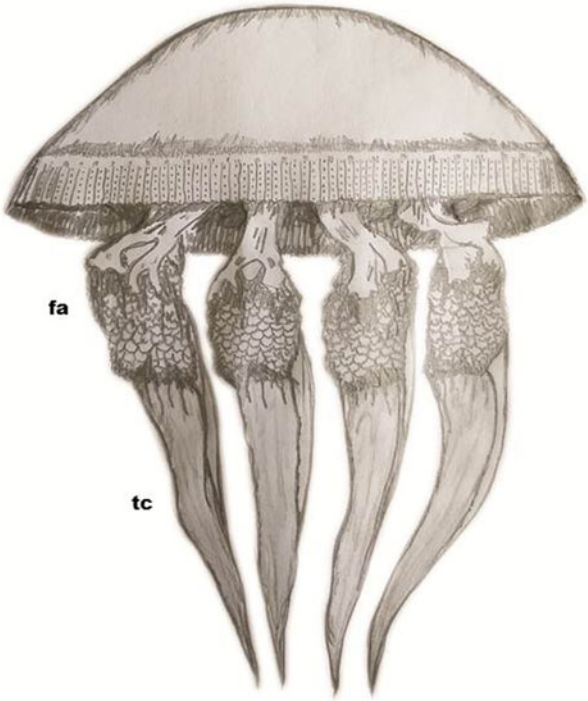

Fig. 4. Schematic diagram of the whole body in lateral view. Only four of the eight oral arms are shown. fa, foliaceous appendage; tc, terminal club.

C. annandalei can be separated from the other species by a combination of the following features: (1) the presence of pointed conical tubercles on the velar lappets, (2) the presence of foliaceous appendages amongst the mouth frills, (3) the high ratio of the distal portion of the oral arm to the naked proximal portion (7.25 ± 0.268) and (4) the high ratio of the terminal club length to the oral arm length (0.48 ± 0.031). It should be noted that although the latter two features can be useful to separate species, they do vary with individual size.

Based on the present study and earlier descriptions, it is evident that the distribution pattern of *Crambionella annandalei* is confined to the Eastern Indian Ocean, in the Bay of Bengal and the Andaman Sea (Figure 2). Locally it is called 'Munthakaya' (in Telugu), and it is caught by gillnets operated by motorized craft at depths less than 50 m along the coast of Andhra Pradesh. This species supports an active jellyfish fishery during its peak swarming season (March to July) and processed jellyfishes are generally exported to South-east Asian countries (Behera *et al.*, 2020).

The colour of living *C. annandalei* has previously been reported as faintly brown (Sarkar *et al.*, 2002; Kitamura & Omori, 2010), whereas our observations show the existence of four distinct colour morphs. Similar observations have been made for *C. helmbiru* from central Java, where Nishikawa *et al.* (2014) reported that the umbrella varied from a uniform (blue) colour to individuals possessing two reddish-brown bands around the margin. A single reddish-brown band on the umbrella margin

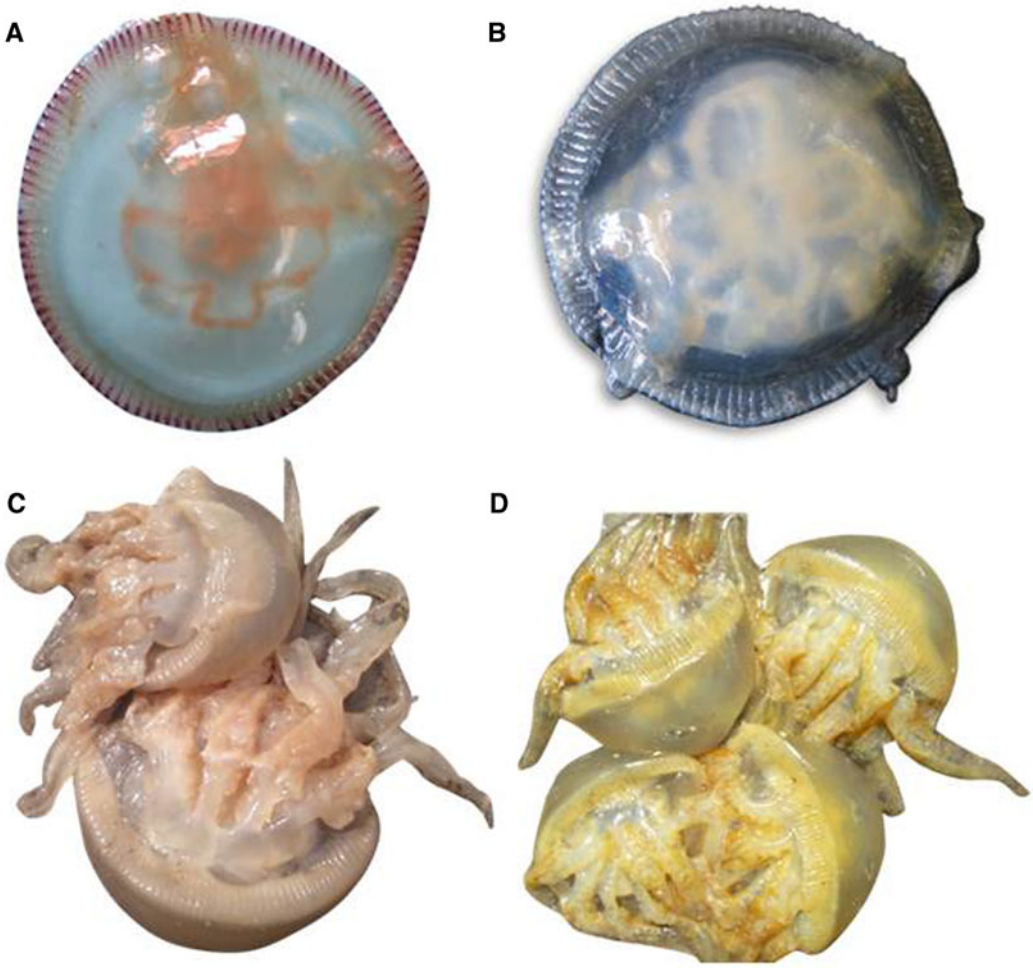

Fig. 5. Colour variation of exumbrella and its margin in *C. annandalei*. (A) Exumbrella translucent white with single reddish brown margin (BD: 98 mm); (B) exumbrella and its margin translucent white (BD: 102 mm); (C) exumbrella and its margin faintly brown (BD: 285 mm); (D) exumbrella and its margin faintly yellow (BD: 275 mm).

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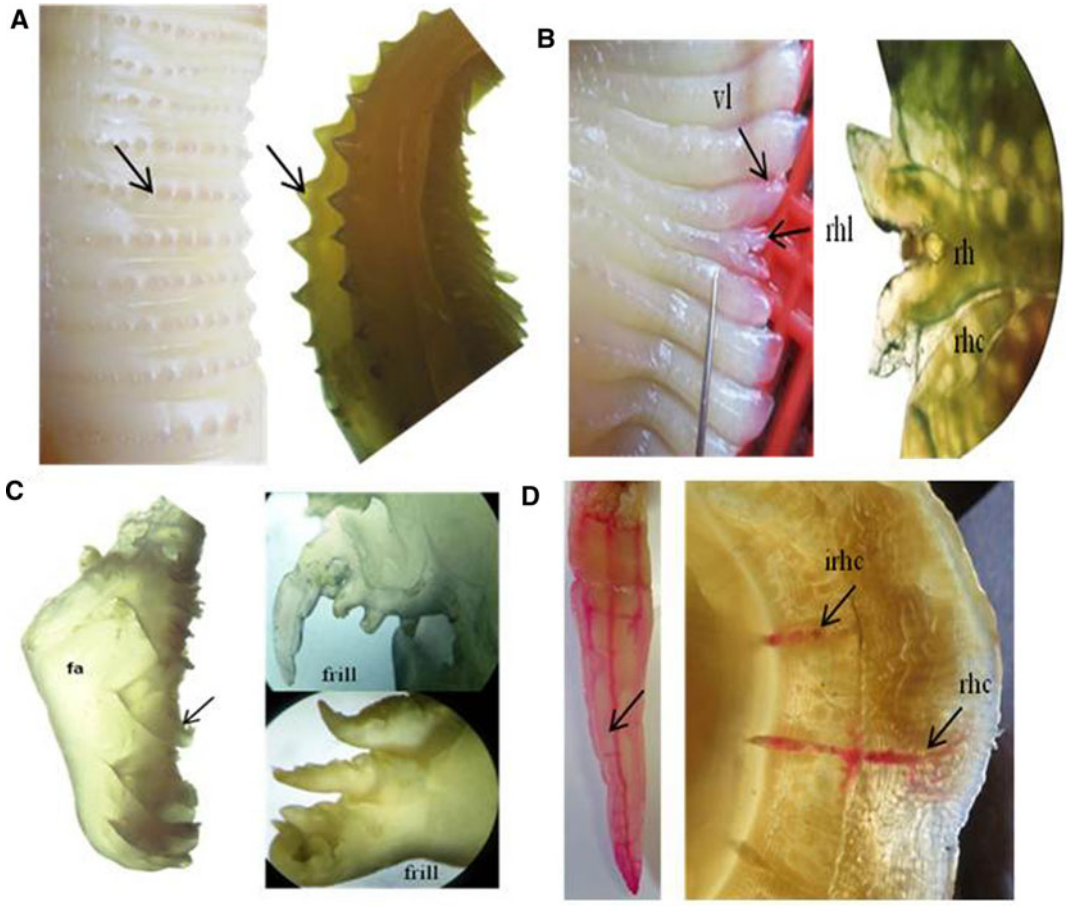

Fig. 6. (A) Presence of pointed conical tubercle on the umbrella margin (left figure) and microscopic view (right figure); (B) vellar and rhopaliar lappets, exumbrella view (left figure) and microscopic view of rhopalium with rhopaliar canal (right figure); (C) microscopic view of foliaceous appendages on trifoliate winged portion of oral arms showing their morphological variation; (D) canal system of terminal club of oral arm and subumbrella view after injecting Rose Bengal solution: axial canal, distal part of oral arm showing the distribution of canals in the terminal appendage (left figure) and point of termination of rhopaliar and inter-rhopaliar canals (subumbrella view) (right figure). vl, velar lappet; rhl, rhophaliar lappet; rh, rhophalia; rhc, rhophaliar canal; fa, foliaceous appendage; irhc, inter-rhophaliar canal.

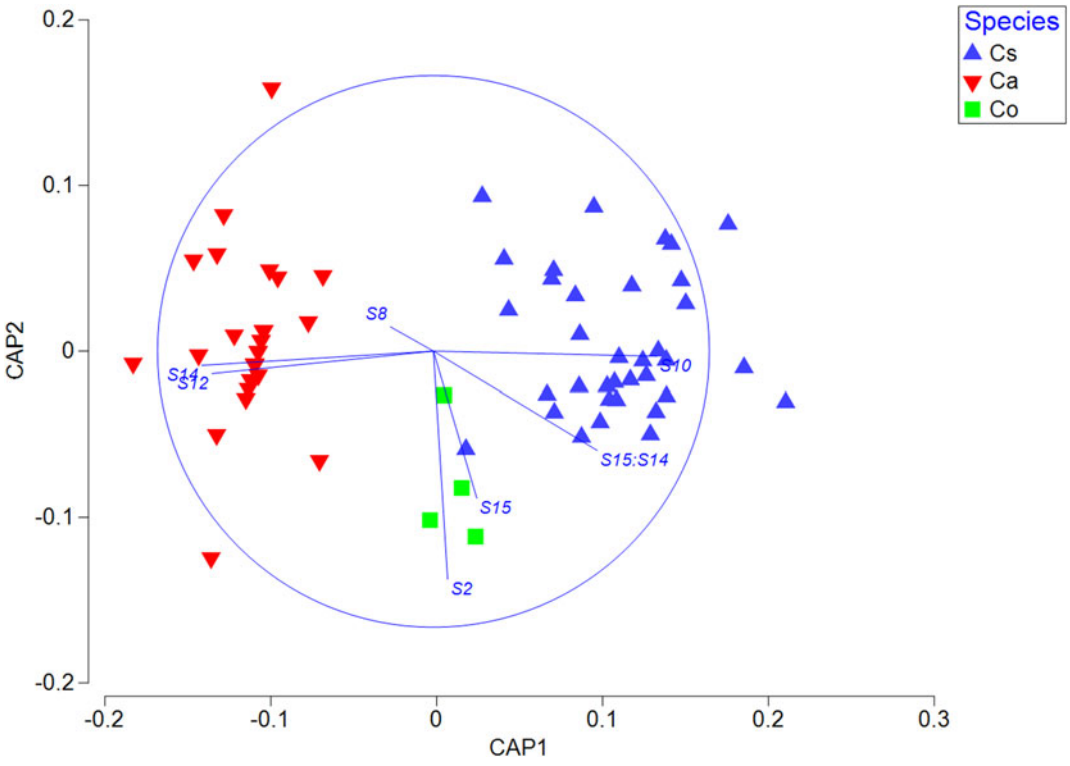

Fig. 7. CAP plot showing the distribution of *Crambionella* specimens with respect to the two CAP axes ($\delta_1^2 = 0.92$, $\delta_2^2 = 0.17$). Vector overlay showing changes in standardized base variables with respect to CAP axes. S2, umbrella height; S8, depth of winged portion of oral arm; S10, length of terminal clubs of oral arm (adaxials); S12, oral disc diameter; S14, width of ostia; and S15, length of ostia and the ratio between length of ostia: width of ostia (S15:S14); Cs, *Crambionella stuhlmanni*; Co, *Crambionella orsini*; Ca, *Crambionella annandalei*.

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Table 3. A character matrix highlighting morphological features that differ among the four *Crambionella* species (Neethling *et al*., 2011; Nishikawa *et al*., 2014) and the *Crambionella* material under the present study

Characters	*Crambionella orsini*	*Crambionella stuhlmanni*	*Crambionella helmbiru*	*Crambionella annandalei*	*Crambionella annandalei* (Present study)
Umbrella diameter (mm)	55–210	62–181	223–342	80–200	65–310
Proportion of umbrella height to umbrella diameter	0.3	0.32 ± 0.03	-	0.3	0.21 ± 0.005
Number of velar lappets in each octant	16	Mode: 12; range: 4–29	14(12–18)	14	14
Pointed conical tubercles on velar lappets	Absent	Present	absent	Present	Present
Number of pointed conical tubercles	Absent	Mode: 12; range: 1–19	absent	14–16	13–19
Proportion of oral disc to external umbrella diameter	0.5–0.6	Mean: 0.32 + 0.04	–	≤0.5	0.32 ± 0.015
Foliaceous appendages amongst mouth frill on distal trifoliate winged portion	Present	Absent	Present	Present	Present
Proportion of distal portion of oral arm to naked proximal portion of oral arm	Three to four times as long	Mean: 2.78 + 0.86	–	More than six times as long	7.25 ± 0.268
Proportion of terminal club length to oral arm length	0.125	Mean: 0.17 + 0.04	0.28	0.5	0.48 ± 0.031
Proportion of ostia to inter-ostia width	1/3–1/2 as wide as inter-ostial columns	Mean: 0.61 + 0.16	–	–	0.36 ± 0.024
Inter-rhopaliar canals termination	Ring canal	Ring canal	–	Ring canal	Ring canal
Number of intra-circular anastomosing canals connected to ring canal	Rare	Rare	–	Rare	Rare
Intra-circular anastomosing canal connections to inter-rhopaliar or rhopaliar canal	Inter-rhopaliar canals	Connections to both inter- and rhopaliar canals	–	–	–
Exumbrella colouration	Light or dark brown, or 4 different patterns	Translucent white with reddish brown single band around exumbrellar margin	Bluish cream with/ without reddish brown spots/two bands around exumbrellar margin	Faintly brown	Brown/Yellowish/ Translucent white with/ without reddish brown single band around exumbrellar margin

has been observed for some *C. stuhlmanni* from the St Lucia Estuary, South Africa (Neethling *et al*., 2011 cf. Perissinotto *et al*., 2013). Although four colour morphs of *C. orsini* were observed by Stiasny (1937), all with a marginal band of pigment, Daryanabard & Dawson (2008) have reported uniformly pigmented individuals from the Gulf of Oman. Scyphozoans are known to display a relatively high level of colour and pattern variation (e.g. Morandini and Marques, 2010), and it could be argued that the relatively high level of localized colour variation observed within the genus *Crambionella* could be an adaptation for concealing this large gelatinous zooplankton from visual predators. Such adaptive phenotypic plasticity would be beneficial for globally distributed scyphozoan jellyfish species which are subjected to significant temperature variation (Nawroth *et al*., 2010).

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References

Anderson MJ, Gorley RN and Clarke KR (2008) *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth: PRIMER-E.

Behera PR, Raju SS, Jishnudev MA, Shubhadeep G and Saravanan R (2020) Emerging jellyfish fisheries along Central South East coast of India. *Ocean and Coastal Management* **191**, 1–7.

https://doi.org/10.1017/S0025315420000703 Published online by Cambridge University Press

Billett DSM, Bett BJ, Jacobs CL, Rouse IP and Wigham BD (2006) Mass deposition of jellyfish in the deep Arabian Sea. *Limnology and Oceanography* **51**, 2077–2083.

Chun C (1896) Beitragezur Kenntnissostafrikanischer Medusen und Siphonophorennach den Sammlungen Dr. Stuhlmann's. *Zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Jahrgang* **13**, 1–19.

Collins AG, Jarms G and Morandini AC (2020) World List of Scyphozoa. *Crambionella* Stiasny, 1921. Accessed through World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=206598 on 2019-04-20.

Daryanabard R and Dawson MN (2008) Jellyfish blooms: *Crambionella orsini* (Scyphozoa: Rhizostomeae) in the Gulf of Oman, Iran, 2002–2003. *Journal of the Marine Biological Association of the United Kingdom* **88**, 477–483.

Kitamura M and Omori M (2010) Synopsis of edible jellyfishes collected from Southeast Asia, with notes on jellyfish fisheries. *Plankton and Benthos Research* **5**, 106–108.

Kramp PL (1956) Medusae of the Iranian Gulf. *Videnskabelige Meddelelserfra Dansk Naturhistorik Forening* **118**, 235–242.

Kramp PL (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom* **40**, 7–382.

Menon MGK (1930) *The Scyphomedusae of Madras and the Neighboring Coast, Vol. 3.* Bulletin of the Madras Government, New Series, Natural History Section.

Menon MGK (1936) *Scyphomedusae of the Krusadai Island, Vol. 1*. Bulletin of the Madras Government, New Series, Natural History Section.

Morandini AC and Marques AC (2010) Revision of the genus *Chrysaora* Peron & Lesueur, 1810 (Cnidaria: Scyphozoa). *Zootaxa* **2464**, 1–97.

Nair KK (1946) Medusae of Travancore and their Correlation with Inshore Fishing, Vol. 32. *Proceedings of the First Indian Science Congress*.

Nawroth JC, Feit KE, Colin SP, Costello JH and Dabiri JO (2010). Phenotypic plasticity in juvenile jellyfish medusa facilitates effective animal fluid interaction. *Biology Letters* **6**, 389–393.

Neethling S, Channing A, Gershwin LA and Gibbons MJ (2011) A modern description of *Crambionella stuhlmanni* (Scyphozoa: Rhizostomeae) from St Lucia Estuary, South Africa. *Journal of the Marine Biological Association of the United Kingdom* **91**, 357–367.

Nishikawa J, Thu NT, Yusoff FM, Lindsay DJ, Mulyadi M, Mujiono N, Ohtsuka S and Nishida S (2009) Jellyfish fisheries in Southeast Asia with special reference to those in Vietnam, Indonesia and Malaysia. *Kaiyo Monthly* **41**, 401–411. [In Japanese].

Nishikawa J, Ohtsuka S, Mulyadi M, Mujiono N, Lindsay DJ, Miyamoto H and Nishida S (2014) A new species of the commercially harvested jellyfish *Crambionella* (Scyphozoa) from central Java, Indonesia with remarks on the fisheries. *Journal of the Marine Biological Association of the United Kingdom* **95**, 471–481.

Perissinotto R, Taylor RH, Carrasco NK and Fox C (2013) Observations on the bloom-forming jellyfish *Crambionella stuhlmanni* (Chun, 1896) in the St Lucia Estuary, South Africa. *African Invertebrates* **54**, 161–170.

Ranson G (1945) Les Scyphomeduses de la collection du Museum National d'Histoire Naturelle Paris. II. Catalogue raisonne; origine des recoltes. *Bulletin du Museum National d'Histoire Naturelle Paris* **16**, 312–320.

Rao HS (1931) Notes on Scyphomedusae in the Indian museum. *Records of the Indian Museum* **33**, 25–62.

Ras V, Neethling S, Engelbrecht A, Morandini AC, Bayha KM, Skrypzeck H and Gibbons MJ (2020) There are three species of Chrysaora (Scyphozoa: Discomedusae) in the Benguela upwelling ecosystem, not two. *Zootaxa* **4778**, 401–438.

Sarkar J, Talukdar S, Dutta and A and Ramakrishna (2002) Occurrence of *Crambionella annandalei* Rao, a scyphozoan jellyfish (Rhizostomae: Catostylidae) from Digha Coast, Midnapore, West Bengal. *Record of Zoological Survey of India* **100**, 31–33.

Stiasny G (1920) Die Scyphomedusen-Sammlung des Naturhistorischen Reichsmuseums in Leiden. III. Rhizostomeae. *Zoologische Mededeelingen* **5**, 213–230.

Stiasny G (1921) Studien uber Rhizostomeen. *Capita Zoologica* **1**, 129–130.

Stiasny G (1922) Ergebnisse der Nachuntersuchungeiniger Rhizostomeer-Typen Haeckel's und Chun's aus dem zoologischen Museum in Hamburg. *Zooogische Mededelingen* **7**, 41–60.

Stiasny G (1937) Scyphomedusae. John Murray Expedition 1933–1934. *Scientific Reports* **4**, 203–242.

Vanhoffen E (1888) Untersuchungen uber semaeostome und rhizostome Medusen. *Bibliotheca, Zoologica* **3**, 1–52.

https://doi.org/10.1017/S0025315420000703 Published online by Cambridge University Press