

First record in Peninsular Malaysia and morphological redescription of *Lychnorhiza malayensis* (Scyphozoa: Rhizostomeae: Lychnorhizidae)

Wan Mohd Syazwan^{1,4}, Liang Boon Low^{2,3} & Mohammed Rizman-Idid^{3*}

Abstract. This study presents the first record of *Lychnorhiza malayensis* Stiasny, 1920, in Malaysian waters since its first discovery in the Java Sea of Indonesia nearly a century ago. Better representation of the species was achieved by the collection of more specimens than previous studies. Thirteen specimens were collected from the midwestern and northeastern coasts of Peninsular Malaysia and their morphology was examined in detail. Morphological descriptions of *L. malayensis* from outside Malaysia and our collection in Malaysia were compared, reviewed and updated. All *Lychnorhiza* species were also compared and differences highlighted. *Lychnorhiza malayensis* can be distinguished from its congeners primarily by the presence of subumbrellar papillae, higher counts of the centripetal canal which tends to anastomose, and the distinctive colour patterns and markings of the umbrella. Intraspecific variations were observed among specimens in terms of different papillae and centripetal canal forms, inter-rhopalial canals that extend beyond or terminating at the circular canal, various colour patterns and markings, the number of velar lappets and size (length and width) of oral arms that were also different from previous descriptions. The morphological redescription of this species will facilitate the identification of this bloom-forming species and contribute to the inventories of marine biological resources in Malaysia.

Key words. jellyfish, taxonomy, intra-species variation, bloom, geographic distribution

INTRODUCTION

Over the past two decades, a noticeable increase in scyphozoan jellyfish blooms has been occurring in marine ecosystems worldwide (Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009). Jellyfish blooms are known for their detrimental impacts on anthropogenic activities related to the sea, including coastal tourism, power plant operation, marine aquaculture industry, and commercial fishing activities (Arai, 2001; Mills, 2001; Purcell et al., 2007; Graham & Bayha, 2008; Richardson et al., 2009; Purcell, 2012). For example, in southeastern Brazil and northern Argentina, the episodic blooms of *Lychnorhiza lucerna* Haeckel, 1880, the most common species of the genus, have affected local fisheries by reducing fishery stocks and catch quality, damaging nets, and preventing fishermen from operating effectively (Schiariti et al., 2008; Nagata et al., 2009; Brotz et al., 2017).

Despite the potential threats of scyphozoan blooms to the local marine ecosystem, taxonomic inventories of scyphozoan jellyfishes in Malaysian waters are still relatively limited. Most available records have been made opportunistically, or as coincidental by-products from non-taxonomical studies, such as envenomation (Williamson et al., 1996), toxicology (Azila & Othman, 1993), symbiotic relationship (Ohtsuka et al., 2010), ingress into power plant (Azila & Chong, 2010) and fisheries (Rumpet, 1991; Omori & Nakano, 2001; Awong et al., 2010; Yusoff et al., 2010; Nishida & Nishikawa, 2011). Some occurrences were also mentioned briefly in book chapters, encyclopaedia and field guide entries (e.g., Nicholas & Yong, 2012). A recent update of taxonomic inventories of scyphozoan jellyfish in Malaysian waters (i.e., Straits of Malacca, South China Sea and Sulu-Sulawesi Sea) has documented a total of 10 species (Rizman-Idid et al., 2016), which represent approximately 5% of the globally known scyphozoan richness (i.e., ~ 200 species; Appeltans et al., 2012; World Register of Marine Species, WoRMS, 2018). However, this number is likely to be a gross underestimate due to several reasons, including that (1) many scyphozoan species in the field are yet to be discovered, described and identified; and 2) species identification is challenging because of poor collections and preservation of voucher specimens, and inadequate reliable taxonomic keys for reference (Rizman-Idid et al., 2016). Nevertheless, Gómez-Daglio and Dawson (2017) have recently provided a robust identification method using detailed morphometric and meristic descriptions of jellyfish morphology. This method can be applied to facilitate species identification of local scyphozoans. The genus *Lychnorhiza* Haeckel, 1880, belongs to the family

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¹Institute of Biological Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia; Email: wanmhsyazwan@yahoo.com

²Institute of Graduate Studies, University of Malaya, 50603 Kuala Lumpur, Malaysia; Email: lblow@hotmail.com

³Institute of Ocean and Earth Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia; Email: rizman@um.edu.my (*corresponding author)

⁴Department of Biology, Faculty of Science, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

Lychnorhizidae Haeckel, 1880, suborder Daktyliophorae Stiasny, 1921, and order Rhizostomeae Cuvier, 1799. The most distinct feature distinguishing *Lychnorhiza* from other two Lychnorhizidae genera (*Anomalorhiza* Light, 1921, and *Pseudorhiza* von Lendenfeld, 1882) is the presence of two to four intra-circular centripetal canals between adjacent radial canals and the absence of terminal appendage on the axial side of oral arm (Kramp, 1961). There have been three *Lychnorhiza* species described to date: *Lychnorhiza lucerna* Haeckel, 1880; *Lychnorhiza arubae* Stiasny, 1920; and *Lychnorhiza malayensis* Stiasny, 1920 (WoRMS, 2018). Another *Lychnorhiza* species from the Colombian Caribbean has recently been discovered and named *Lychnorhiza* sp. aff. *L. lucerna* because this new undescribed species bears some resemblance to *L. lucerna* (Cedeño-Posso & Pérez, 2013). Taxonomical confusion has persisted over the genus *Lychnorhiza* and its species. For example, three doubtful genera (*Rhacophilus*, *Crambessa*, and *Cramborhiza*) and two nominal genera (*Rhizostoma* and *Catostylus*) have been used to refer to the genus *Lychnorhiza* (Kramp, 1961; Morandini, 2009). However, since *Lychnorhiza* and its type species, *L. lucerna*, are more widely used among these synonyms, Morandini (2009) proposed that both the generic and specific names should be conserved in order to maintain nomenclatural stability. The distribution of the genus *Lychnorhiza* is restricted to shallow tropical waters. *Lychnorhiza lucerna* is widely distributed along Argentinian and Brazilian coasts (Stiasny, 1932; Kramp, 1961; Mianzan & Cornelius, 1999; Morandini et al., 2005; Schiariti et al., 2008). *Lychnorhiza arubae* has only been recorded in Aruba Island, off the coast of Venezuela (Stiasny, 1920, 1921), and has never been found again since the earliest descriptions.

Lychnorhiza malayensis was discovered within the Malay Archipelago (Stiasny, 1920, 1921), specifically in the Java Sea, Indonesia. Since then, the occurrence of *L. malayensis* has been reported several times in the same region (Stiasny, 1932; Mujiono, 2010) and along the Indian coasts, including Madras, Thiruvananthapuram, and Goa (Menon, 1930; Nair, 1951; Jeyabaskaran et al., 2016). Recently this species has been documented in Andaman Sea and Gulf of Thailand (Department of Marine and Coastal Resources Thailand, 2018). Unfortunately, the historical descriptions of *L. malayensis* by Stiasny (1920, 1921, 1932), Menon (1930) and Nair (1951) were based on only a few specimens, and sometimes the number of specimens was not mentioned. The specimens could also be either difficult to trace or badly damaged. Apart from these historical descriptions, the identity of *L. malayensis* mentioned in recent literature (e.g., Mujiono, 2010; Jeyabaskaran et al., 2016) is often dubious and not substantiated by good descriptions, pictures, or voucher specimens. Therefore, the present study does not examine museum collections but relies on species descriptions from the older, more robust literature. Furthermore, specimens from the type locality have not been sampled, since the Java Sea is beyond the geographic scope of this study.

Here we present the first record of *L. malayensis* in Malaysian waters. In order to update and complement the historical descriptions of the species, we re-examined morphological

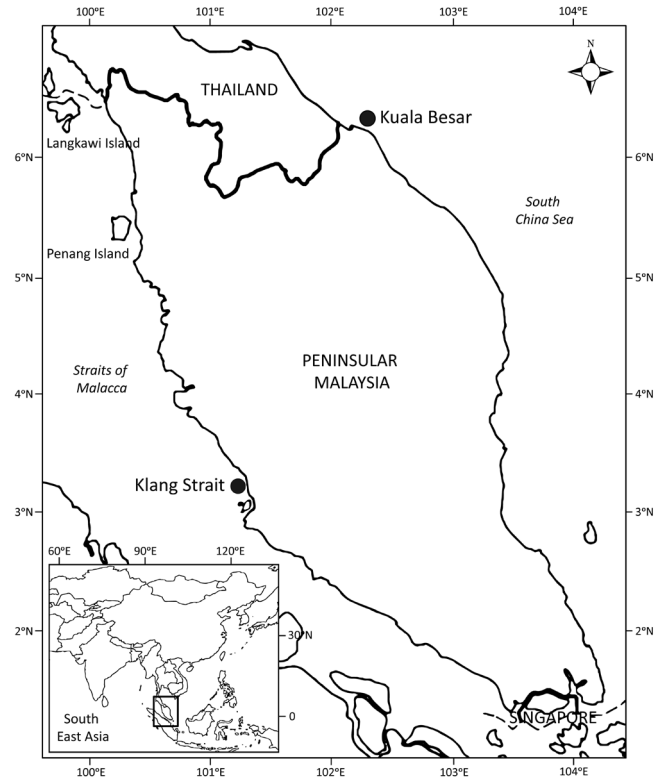


Fig. 1. Map showing sampling locations of *Lychnorhiza malayensis* in Peninsular Malaysia, comprising Klang Strait ($3^{\circ}10'06.8''\text{N}$ $101^{\circ}16'44.4''\text{E}$) and Kuala Besar ($6^{\circ}14'18.4''\text{N}$ $102^{\circ}14'46.4''\text{E}$).

features in detail and re-described the species based on specimens collected from two different localities in Malaysia.

MATERIAL & METHODS

Field collections were made at two localities (Fig. 1), Klang Strait (midwestern Peninsular Malaysia, $3^{\circ}10'06.8''\text{N}$ $101^{\circ}16'44.4''\text{E}$) on 4 October 2010, and Kuala Besar (northeastern Peninsular Malaysia, $6^{\circ}14'18.4''\text{N}$ $102^{\circ}14'46.4''\text{E}$) on 20 February 2014 during the flood tide in daylight. Samples from Klang Strait were collected from stationary commercial bag nets (known locally as “pompang”) that were set against the currents covering the whole water column. The mesh size ranges from 20 mm to 50 mm, with mouth opening of approximately 6 m and vertical opening that changes proportionally with tidal water height (< 10 m). Samples from Kuala Besar were collected at depth approximately 1 m from surface using dip net with mesh size of 5 mm. Although collection by hand or diving is the best jellyfish sampling method to minimise damage, the use of the bag net is more suitable in the muddy and highly turbid waters of Klang Strait. More samples could also be collected from a wider depth range using this method. Samples were handled with care to minimise damage. Jellyfish were unloaded from the nets into containers filled with seawater still on the boat. On land, samples were instantly photographed to record live colouration and then transferred into individual plastic bags filled with 5% formalin (neutralised) seawater solution for further morphological observation. Only samples in good condition with no or minimal damage were retained

as voucher specimens. Specimens were tagged, catalogued and deposited in the Zoological Museum, Institute of Biological Sciences, of University of Malaya (MZUMCS). Ninety-two detailed morphological characters including colouration of preserved specimens were analysed and measured, and their respective character states were recorded within a week after preservation (Appendix 1). A set of photographs were taken for those structures to facilitate the morphological examination and collection of morphological data (Appendix 2). All morphological examinations and photographic procedures were modified from Gómez-Daglio and Dawson (2017). Specimens were photographed using a digital camera (Olympus PEN Lite E-PL5, lens 18–105 mm) against a colour reference chart (Tiffen Q-13 Colour Separation Guide), scale, and reference number for identification. Briefly, each specimen was photographed using two methods. Firstly, the specimen was suspended using wires in a transparent glass aquarium (50 cm × 30 cm) filled with water against a black background, so that the specimen appeared to be floating naturally. Secondly, the specimen was placed on a flat transparent acrylic stage and two images of each specimen were recorded: (1) with the exumbrellar surface facing upward; and (2) with the subumbrellar surface facing upward.

Compound microscope or magnifying glass was used to observe minute structures (e.g., rhopalium, gastric filaments and muscle folds). Visualisation of canal networks was enhanced by carefully injecting red food dye into the canals. To determine the sex and maturity status, a thin sheet of gametogenic tissue was dissected from gonad, laid on a glass slide and examined using a compound microscope. The morphological data was tested for normality and homoscedasticity and invariant characters were excluded from subsequent analyses. To facilitate analysis of data recorded in different units (e.g., length and number) and scales (e.g., shape and colour), all data were standardised prior to analyses using default functions in Primer V6 (see Clarke & Warwick, 2001). Morphological similarity was tested and plotted using principal component analysis (PCA) in PRIMER V6 software (Clarke & Gorley, 2006).

TAXONOMY

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Petersen, 1979

Class Scyphozoa Goette, 1887

Subclass Discomedusae Haeckel, 1880

Order Rhizostomeae Cuvier, 1799

Family Lychnorhizidae Haeckel, 1880

***Lychnorhiza* Haeckel, 1880**

Type species. *Lychnorhiza lucerna* Haeckel, 1880.

Diagnosis. Oral arms without axial terminal clubs, with or without filaments, eight radial canals reaching bell margin, while another eight radial canals only reaching circular canal; two to four centripetal canals between the adjacent radial canals.

***Lychnorhiza malayensis* (Stiasny, 1920)**

(Figs. 2–4)

Lychnorhiza malayensis – Stiasny, 1920: 226 (type locality: Java Sea, Indonesia); Stiasny, 1921: 122, pl. 2, fig. 9 (redescription of the type specimen); Menon, 1930: 17, pl. 2, fig. 8a–c (Madras, India); Stiasny, 1932: 89–95, figs. 1–4 (Java Sea, Indonesia); Nair, 1951: 74 (Trivandrum, India).

Material examined. 6 mature males, 2 mature females (bell diameter 98–155 mm) (MZUMCS 0255–0262), Klang Strait (3°10'06.8"N 101°16'44.4"E), bag net, coll. W.M. Syazwan, 4 October 2010. 1 immature male, 2 immature females, 2 sex-unidentified (bell diameter 45–60 mm) (MZUMCS 0264–0268), Kuala Besar (6°14'18.4"N 102°14'46.4"E), dip net, coll. W.M. Syazwan, 20 February 2014.

Description. Bell hemispherical in live specimens, more flattened in preserved ones (Fig. 2A). Bell diameter ranges from 45 to 155 mm. Exumbrellar surface with fine granules. At the margin, generally eight (four pairs) of almost symmetrical, slightly tapered velar lappets in each octant (Fig. 2C). Velar lappets separated by clefts formed by furrows with thin membranous base; each pair are separated by shorter and shallower furrows. Eight tear-drop shaped rhopalia; four perradial and four interradian. Each rhopalium situated in a bell-shaped rhopalium pit with radiating furrows at the marginal cleft; flanked laterally by two rhopalium lappets, more pointed, shorter and narrower than velar lappets (Fig. 2E).

Oral disc almost quadratic in shape; perradial and interradian diameters are $\frac{1}{3}$ and $\frac{1}{2}$ as wide as the bell diameter, respectively (Fig. 2C). Oral disc without appendages; supported by four interradian, broad-based pillars (Fig. 2C). Four perradial ostia lead from the subgenital cavity; located between two pillars, crescent-shaped, about as wide as the oral pillar. Three to five subumbrellar papillae projected around each ostium: two or three papillae positioned at the medial part, while one or two at the periphery (Fig. 2C, see also Fig. 3). Medial papillae resting on the rhopalium canal at the centre of ostium, highly varied in shape (oblong, ovoid, trapezoid, hammer-shaped) and not uniform in size. The peripheral papillae (one on each ostium's margin) lie mostly within the ostium, uniform, smaller and shorter than the medial papillae; absent in some juvenile specimens. Papillae surface generally smooth or finely granulated.

Gastrovascular cavity cruciform in shape; with rounded corners, more dilated peripherally; diameter at perradial axis always slightly less than half the diameter at interradian axis (Fig. 2D). Perradial diameter of gastrovascular cavity about $\frac{1}{4}$ as wide as bell diameter. Gonad four in number, perradial, crescentic with concavity facing outward toward bell margin, entirely closed (Fig. 2D). Each gonad comprised of heavily

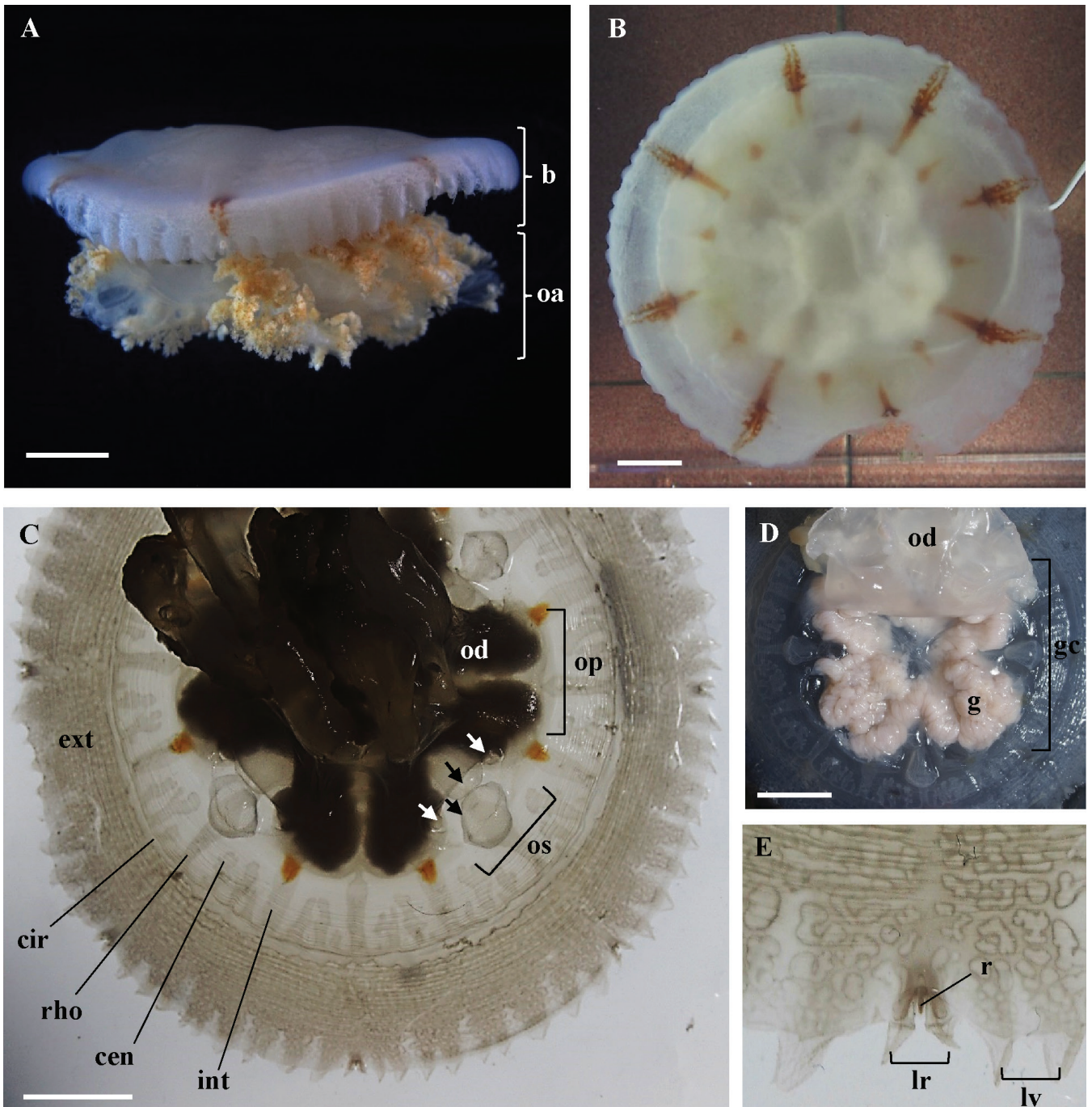


Fig. 2. Photographs showing different views and morphological characters of *Lychnorhiza malayensis* (fixed with 5% formaldehyde). A, lateral view of the whole body; B, exumbrellar view of the smooth bell surface; C, subumbrellar view of the bell showing main visible characters; D, subumbrellar view of the bell showing the exposed gastrovascular cavity; E, close-up subumbrellar view of the rhopalium and lappets. b, bell; oa, oral arm; od, oral disc; op, oral pillar; os, ostium; ext, extra-circular canal; cir, circular canal; cen, centripetal canal; rho, rhopalium canal; int, inter-rhopalium canal; gc, gastrovascular cavity; g, gonad; r, rhopalium; lv, velar lappet; lr, rhopalium lappet. Black arrow, medial papillae; white arrow, peripheral papillae. Scale bars = 20 mm.

folded tissue sheets, lying in the floor of gastrovascular cavity, associated with the inner side of oral disc and pillars. Gastric cirri (i.e., filaments) line the inner side of the gonad folds. Gonad visible as a cruciform-shaped structure from exumbrellar side. Matured gonads plump, immature ones thinner. Maturity reached when bell diameter ~ 90 mm. All specimens from Klang Strait mature (two females, six males); all specimens from Kuala Besar immature (two females, one male, two sex-unidentifiable).

A circular canal at $\frac{1}{3}$ of radial distance from the bell margin (Fig. 2C). 16 irregularly-sized, bottle-shaped radial canals present, comprising eight rhopalium canals (also known as perradial canals) extending to the bell margin, and eight slightly broader inter-rhopalium canals (inter-radial canals) terminating at the circular canal. Some inter-rhopalium canals appear to extend beyond the circular canal (as shown by the rhopalium canals), but on closer inspection are thinner, and seem to be more subdivided than those of the rhopalium canals. Rhopalium canals broader at intra-circular than those

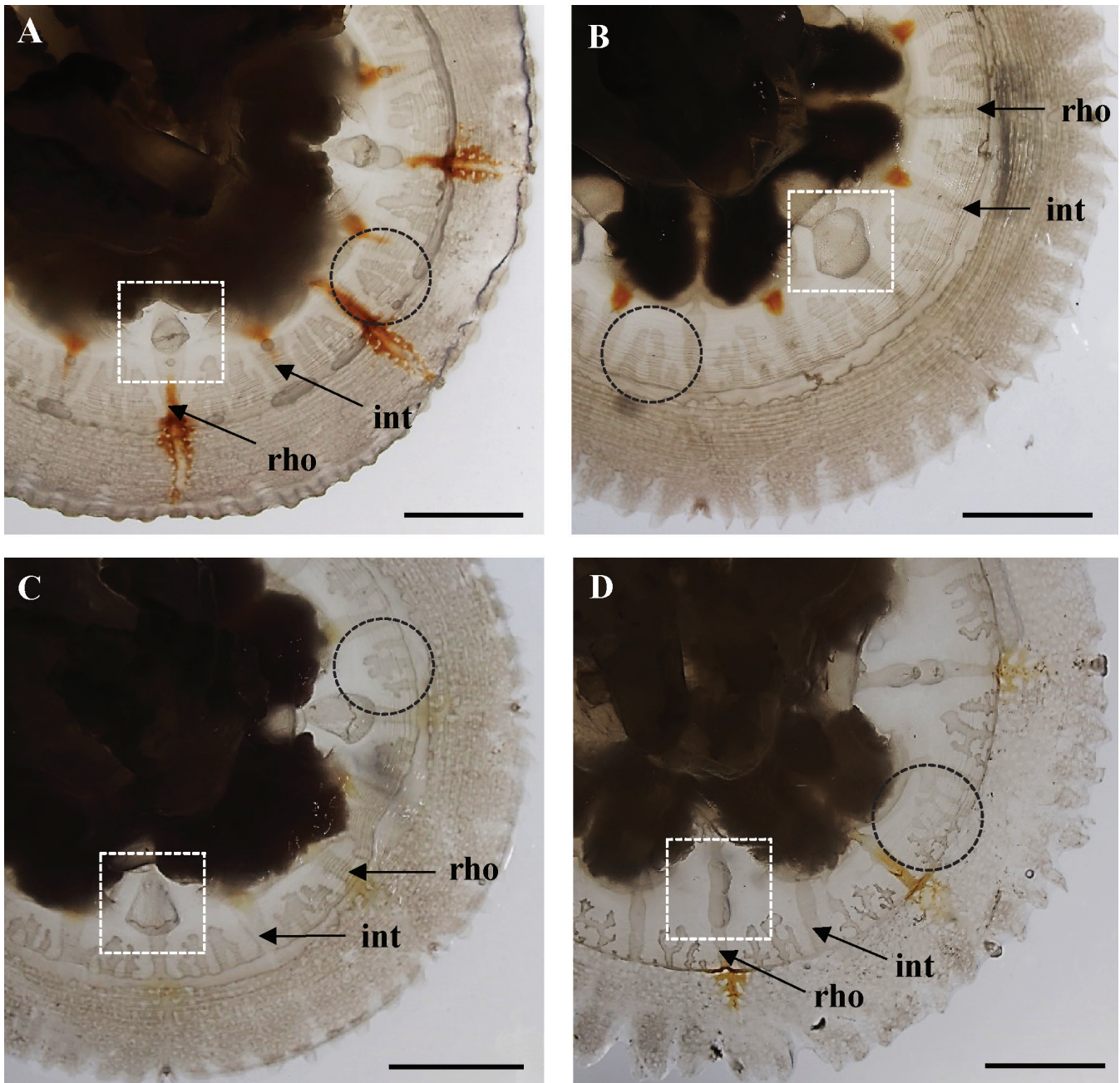


Fig. 3. Morphological variation among individuals observed in medial papillae (white box), centripetal canals between radial canals (black circle) and radial canal (i.e., rhopalial and inter-rhopalial canal) as shown in the subumbrellar view of specimens MZUMCS 0255–0258. A, specimen MZUMCS 0255 showing the ovoid-shaped papillae, two centripetal canals that terminate abruptly, entirely coloured rhopalial canals and partially coloured inter-rhopalial canals (near the gastrovascular cavity). B, specimen MZUMCS 0256 showing the oblong-shaped papillae, three centripetal canals that terminate abruptly, entirely colourless rhopalial canals and partially coloured inter-rhopalial canals (only coloured near the gastrovascular cavity). C, specimen MZUMCS 0257 showing the trapezoid-shaped papillae, three lightly anastomosed centripetal canals, faintly coloured rhopalial and inter-rhopalial canals. D, specimen MZUMCS 0258 showing the oblong-shaped papillae, four highly anastomosed centripetal canals, partially coloured rhopalial canals (near the circular canal) and entirely colourless inter-rhopalial canals. rho, rhopalial canal; int, inter-rhopalial canal. Scale bars = 20 mm.

at extra-circular part. Intra-circular network between adjacent radial canals comprises centripetal canals which communicate with the circular canal, but not with the adjacent rhopalial and inter-rhopalial canals. Number of centripetal canals (adradial canals) in between adjacent radial canals ranges from two to five in adults (Fig. 3), and from one to five in juvenile specimens. Centripetal canals generally proportional to bell diameter in terms of width; always narrower than radial canals; more or less parallel; not uniform in length,

terminating abruptly, but occasionally showing tendency to anastomose. Extra-circular canal network finely meshed, uniformly anastomosed, and becoming denser and narrower towards the periphery of bell. The penetration of this anastomosis network reaches the marginal lappets, but not all the way to the tips.

A well-developed circular muscle area of ca. 42–72 muscle folds extends distally from the outer base of pillars

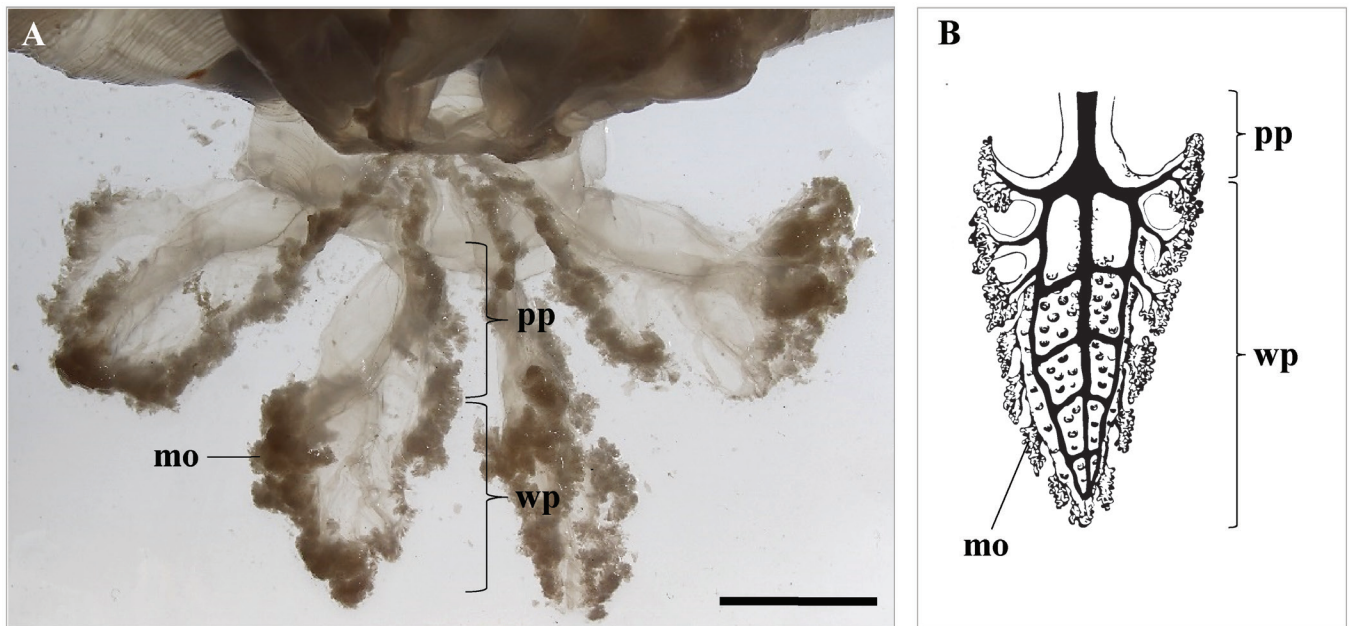


Fig. 4. Differences in oral arm morphology between *Lychnorhiza malayensis* from Klang Strait and the Java Sea. A, lateral view of specimen MZUMCS 0256 from Klang Strait showing four of eight oral arms. B, illustration of a single oral arm of *L. malayensis* from the Java Sea by Stiasny (1932) (scale not available). The length of the winged portion of *L. malayensis* from Klang Strait is shorter (half of total arm's length) than those described from the Java Sea (3/4 of total arm's length). pp, proximal portion of oral arm; wp, winged-portion of oral arm; mo, frills of mouthlet. Scale bars = 20 mm.

till the marginal lappets, covering approximately $\frac{2}{3}$ of the subumbrellar surface (Fig. 2C). The musculature not interrupted over the 16 radial canals.

Eight oral arms, adradial, not coalesced with each other; each slightly shorter than the radius of the bell. Proximal portion half of the arm's total length, laterally flattened, outer margin without frills. The remaining portion divided into three broad wings (one inner and two outer), more flattened than the proximal part (Fig. 4A). The edges of the three wings much-folded with frills containing numerous mouthlets among them. Mouth frills of inner wings reaching upward to inner margin of proximal portion and centre of oral disc. Oral arms lacking appendages. Oral arms of all immature specimens (bell diameter < 60 mm) not well-developed.

Live and preserved individuals display minimal differences in colouration. Bell whitish. Exumbrellar surface in some specimens ornamented with reddish-brown spots or markings along the interradial and perradial axes that radiate from apex towards bell margin (Fig. 2A, B). Rhopaliar canals either colourless (Fig. 3B) or reddish-brown, with intense markings when adjoining circular canals (Fig. 3A, C, D). Inter-rhopaliar canals only coloured in parts, specifically when adjoining the gastrovascular cavity (Fig. 3A–C); generally fainter than the rhopaliar canal, while colourless in some specimens (Fig. 3D). Oral arms whitish, mouth frills whitish to faintly brown. Gonads whitish to faintly brown.

Morphological variation. A remarkable variation among individuals was observed in some key characters: (1) number of velar lappet per octant; (2) number, length and formation of centripetal canals; (3) number and shape of subumbrellar papillae; (4) the extension of inter-rhopaliar canal beyond

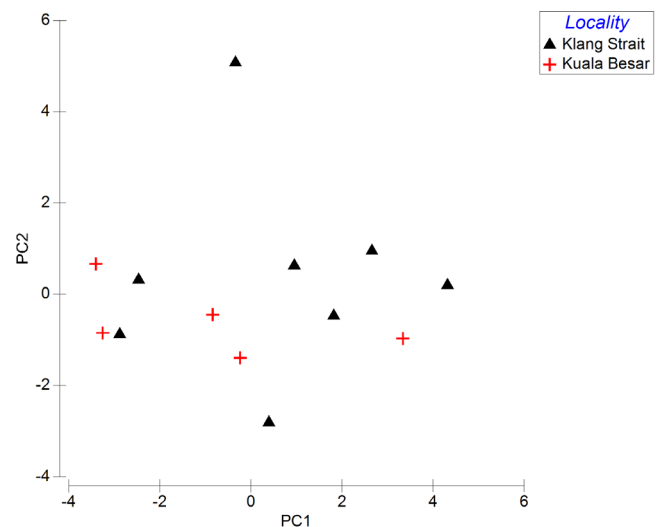


Fig. 5. Two-dimensional principal component analysis (PCA) of 10 meristic characters (f4, f27, f29–33, f44, f45, f90) and 11 categorical characters (f51, f52, f80, f81, f83, f84, f87–89, f91, f92) indicating morphological similarity among *Lychnorhiza malayensis* individuals from Klang Strait (n = 7) and Kuala Besar (n = 5). PC1 explains 31.2 % of observed variation. PC2 explains 16% of observed variation. The character states are listed in Appendix 1.

circular canal; and (5) colouration of live and preserved specimens. The intraspecific morphological variations were persistent in both localities (Klang Strait and Kuala Besar) but individuals did not differ between sites. Principal component analysis (PCA) of these key characters did not suggest a clear separation between *L. malayensis* individuals from Klang Strait and Kuala Besar (Fig. 5).

Other remarks. During a subsequent monthly ecological survey in Klang Strait from January until December 2011, *L.*

malayensis occurred during May 2011 (Southwest Monsoon) and later during October–November 2011 (Northeast Monsoon). Abundance was significantly greater during the latter period. This species also forms part of the commercial fisheries by-catch along with other scyphozoan jellyfishes, such as *Cyanea* sp., *Phyllorhiza punctata*, *Lobonemoides robustus*, and *Rhopilema esculentum*. At the northwestern Peninsular Malaysia (i.e., Langkawi Island and Penang Island), this species is commonly encountered in swarms with *Acromitus flagellatus*.

DISCUSSION

This first record of *L. malayensis* from Peninsular Malaysia underscores the general lack of taxonomic and ecological study of jellyfish in the country. The species may not be rare in Malaysian waters because after finishing the present study, our team has recently collected specimens in Langkawi Island and Penang Island, located in the northwestern Peninsular Malaysia (Fig. 1). Therefore, the geographical distribution of *L. malayensis* now extends from the western and eastern coasts of India (Menon, 1930; Nair, 1951; Jeyabaskaran et al., 2016), the Andaman Sea and Gulf of Thailand (Department of Marine and Coastal Resources Thailand, 2018), the Java Sea (Stiasny, 1920, 1921, 1932), to the Strait of Malacca and the South China Sea (present study). While *L. malayensis* has a wide distribution area, it is geographically separated and distant from another large marine area (Central and South America) that currently harbours three *Lychnorhiza* species (Table 2).

Morphological distinction among *Lychnorhiza* species is primarily based on the exumbrellar surface, number of velar lappets, presence of subumbrellar papillae, formation of centripetal canals, interruption of circular musculature on radial canals, size of oral arms, and live colouration (Table 2). *Lychnorhiza malayensis* shares more similarities with *L. arubae* by having eight velar lappets (fewer in *L. lucerna* and *Lychnorhiza* sp. aff. *L. lucerna*), circular musculature that is not interrupted over radial canals (interrupted over radial canals in some *L. lucerna* and *Lychnorhiza* sp. aff. *L. lucerna*), and smaller proportion of oral arms to bell diameter relative to *L. lucerna* and *Lychnorhiza* sp. aff. *L. lucerna* (Table 2). *Lychnorhiza lucerna* is similar to *L. arubae* by the presence of appendages and filaments on oral arms and oral disc (absent in *L. malayensis* and *Lychnorhiza* sp. aff. *L. lucerna*). However, the presence (or absence) of oral appendages is not a reliable characteristic to distinguish *Lychnorhiza* species. It is known that the oral appendages and filaments in many scyphozoans including *L. lucerna* are deciduous and easily detached when forceful collection techniques such as the trawl net and bag net are used (Mianzan & Cornelius, 1999; Morandini, 2003).

Lychnorhiza malayensis can be distinguished from other *Lychnorhiza* species based on the following characteristics: (1) smooth exumbrellar surface (the exumbrella of other species is usually with granulation or fine projections); (2) presence of subumbrellar papillae close to the genital

ostium (absent in other species); (3) centripetal canals more numerous, narrower, and tend to anastomose (fewer, broader, and rarely anastomose in other species); and (4) distinctive colour patterns and markings on subumbrella and exumbrella.

Scyphozoans often display considerable intraspecific variation between geographically isolated populations (Dawson & Martin, 2001; Bolton & Graham, 2004; Dawson, 2005) and among individuals within the same population (Neethling et al., 2011; Nishikawa et al., 2015). Although individuals of *L. malayensis* in the present study were collected from Klang Strait and Kuala Besar, no clear morphological differences were observed between samples from the two locations. However, inter-individual differences were evident for each site.

The first character with intraspecific variation is the subumbrellar papillae. This feature (often found within ostium) is exclusive to *L. malayensis* and absent from congeners. This character varies in number and shape (Figs. 2C, 3). Total number of medial and peripheral papillae per ostium ranges from three to five but may be lower when some immature specimens lack the peripheral papillae. This number agrees with the number of papillae (per ostium) observed in the type specimen of *L. malayensis* (0–3 papillae; Stiasny, 1921) and other specimens that were later reported from the Indian coasts (four papillae; Menon, 1930) and Java, Indonesia (0–4 papillae; Stiasny, 1932) (see Table 2). We also detected more papillae shapes in the current specimens than previously described (i.e., ovoid and oblong; Stiasny, 1932), with the addition of trapezoid- and hammer-like shapes. Inter- and intraspecific variations of centripetal canal persist among *L. malayensis* and its congeners (Tables 1, 2). Previously, Stiasny (1932) has reported large variations of the centripetal canals among the *L. malayensis* individuals from the Java Sea in terms of number (between adjacent radial canals), length and formation, ranging from two to five canals; with inconsistent length; canal formations that tend to anastomose or terminate abruptly at the end. The description is consistent with the current observation (Fig. 3). Some juvenile individuals from Kuala Besar were also observed to have a single centripetal canal between adjacent radial canals, suggesting a possible ontogenetic change, rather than an intraspecific variation. The number of centripetal canals (between adjacent radial canals) in observed specimens apparently overlaps with those described for other *Lychnorhiza* species (Table 2), being two in *L. arubae* (Stiasny, 1921), three to four in *Lychnorhiza* sp. aff. *L. lucerna* (Cedeño-Posso & Pérez, 2013) and two to four in *L. lucerna* (Morandini, 2003). For *L. lucerna*, the centripetal canals were also reported to form unusual “bifurcations and fusions” (Morandini, 2003), which were also observed in *L. malayensis*. Another interspecific variation is the extension of inter-rhopalial canals. *Lychnorhiza* is characterised by inter-rhopalial canals that terminate at the circular canal (Kramp, 1961). In the current specimens, the staining patterns of inter-rhopalial canals sometimes extend beyond the circular canal until the bell margin. However, these extensions are less prominent, thinner, and more subdivided than the rhopalial canal extensions. Similar variation was previously highlighted

Table 1. Main characters of *Lychmorhiza malayensis* observed in the present study compared to conspecifics recorded from different geographical localities based on the literature.

Character	Present study	Stiasny (1920, 1921)*	Stiasny (1932)	Menon (1930)
No. of examined individuals	13	1	3	Not mentioned
Bell diameter	98–155 mm	42 mm	40–75 mm	100 mm
Number of velar lappets	7–9 per octant	8 per octant	8 per octant	8–9 per octant
Subumbrellar papillae (per ostium)	0–5 in total; 2–3 medial, 0–2 peripheral; peripheral smaller and shorter than medial; ovoid, oblong, trapezoid or hammer-like in shape; surface smooth or granulated	0–3 in total; 0–1 medial, 0–2 peripheral	0–4 in total; 0–2 medial, 0–2 peripheral; ovoid and oblong in shape; surface smooth or granulated	4 in total; 2 medial, 2 peripheral
Circular musculature	Continuous; 42–72 muscle folds	Continuous	Not mentioned	Not mentioned
Oral arms	Total length less than half of bell diameter; length of winged portion half of total arm's length, broad and laterally flattened	Total length as long as bell diameter; winged portion as long as 3/4 of total arm's length	Total length as long as bell diameter; winged portion as long as 3/4 of total arm's length	Total length as long as 2/3 of bell diameter; length of winged portion slightly more than half of total arm's length
Inter-rhopalial canal extension	Rarely extend beyond the circular canal; extension is less prominent than that of the rhopalial canal	Do not extend beyond the circular canal	Rarely extend beyond the circular canal	Not mentioned
Centripetal canals between adjacent radial canals	Number 1–5; inconsistent length; the end terminating abruptly, but some tend to anastomose	Number 4; almost parallel; the end terminating abruptly, but some tend to anastomose	Number 2–5; inconsistent length; the end terminating abruptly, but some tend to anastomose	Number 2–4, the end terminating abruptly, but some tend to anastomose
Colouration	Bell whitish, exumbrella sometimes with reddish-brown spots or radiating lines from apex towards margin; radial canals entirely colourless or reddish-brown in parts (i.e., when the rhopalial canals adjoining the circular canal or the inter-rhopalial canals adjoining the gastrovascular cavity); oral arms whitish, mouth frills whitish to slightly brownish; gonad whitish to slightly brownish	Almost colourless	Bell whitish or yellowish; rhopalial canals entirely colourless; inter-rhopalial canals coloured in reddish-brown when adjoining the stomach cavity	Rhopalial canals entirely coloured in reddish-brown, with intense markings when meeting the adjoining canals; inter-rhopalial canals only coloured in parts
Distribution	Midwestern and northeastern coasts of Peninsular Malaysia	Java Sea, Indonesia	Java Sea, Indonesia	Madras, India
Other remarks	8 matures, 5 immatures; greater abundance during Northeast Monsoon	Immature	All specimens are immature	Highly infected with copepods and flatworms

*description is based on the type specimen of *L. malayensis*

Table 2. Main distinguishing characters among *Lychnorhiza* species.

Character	<i>Lychnorhiza</i> sp. aff.		
	<i>L. malayensis</i>	<i>L. lucerna</i>	<i>L. arubae</i>
Exumbrellar surface	With fine granules	With fine granules or sharp-pointed projections	With fine granules or sharp-pointed projections
Number of velar lappets	8 (4 pairs) per octant	4 per octant, possibly extra in older individual	8 (4 pairs) per octant
Filaments on oral disc	Absent	Present, but deciduous	Present
Subumbrellar papillae	0–3 medial, 0–2 peripheral; peripheral smaller and shorter than medial; ovoid, oblong, trapezoid or hammer-like in shape; surface smooth or granulated	Absent	Absent
Circular musculature	Continuous	Interrupted on radial canals, while some are continuous	Continuous
Oral arms	Total length ranges from half to as long as bell diameter; winged portion ranges from half to 3/4 of total arm's length, broad and laterally flattened	Total length as long as bell diameter; winged portion 3/4 of total arm's length	Total length as long as half of bell diameter; winged portion 2/3 of total arm's length
Appendages on oral arms	Absent	Numerous, thick, long filaments, deciduous	Few short filaments
Centripetal canals between adjacent radial canals	1–5; inconsistent length; the end blindly terminating, but some tend to anastomose	2–4, few tend to anastomose at the end	2
Colouration	Bell whitish, exumbrella sometimes with reddish-brown spots or radiating lines from apex towards margin; radial canals entirely colourless or reddish-brown in parts; marginal lappets not coloured; oral arms whitish, mouth frills whitish to slightly brownish; gonad whitish to slightly brownish	Bell colourless, brown, pale brown or blue; marginal lappets brown, red or blue; oral arms colourless; mouth frills pale brown or colourless; gonad whitish, cream-coloured or greenish	Bell whitish with eight blue-purple stains, two in each arch of the gonad; marginal lappets not coloured; oral arms whitish; gonad blue or cream-coloured
Distribution	Midwestern and northeastern coasts of Peninsular Malaysia, Java Sea, Andaman Sea, Gulf of Thailand and Indian coasts	Argentinian and Brazilian coasts	Colombian Caribbean waters Aruba Island, off Venezuelan coast
Source	Stiasny, 1920; Stiasny, 1921, Menon, 1930; Stiasny, 1932; Kramp, 1961; present study	Stiasny 1921, 1932; Kramp, 1961; Mianzan & Cornelius, 1999; Morandini, 2003	Stiasny, 1920, 1921; Kramp, 1961

in the description of one of the three *L. malayensis* specimens from the Java Sea (Stiasny, 1932). However, such variation was not mentioned in the descriptions of the type specimen (Stiasny, 1920, 1921) and *L. malayensis* from the Indian coasts (Menon, 1930). Colour variations also persist in the radial canals (colourless to reddish-brown), mouth frills (whitish to slightly brownish) and gonad (whitish to slightly brownish), with minimal colouration differences between live and preserved specimens. There were more colour variations, patterns and markings observed than previously reported (Stiasny, 1921, 1932; Menon, 1930; see Table 1). The prominent colouration of radial canals (i.e., rhopaliar canals and inter-rhopaliar canals) on subumbrellar surface was previously described by Menon (1930) as “the rhopaliar canals are entirely coloured in reddish-brown, with intense markings when rhopaliar canals meet the adjoining canals (i.e., circular canal), whereas inter-rhopaliar canals only coloured in parts”. We found that the description above is not entirely accurate, since some of the rhopaliar and inter-rhopaliar canals of our specimens were entirely colourless (Fig. 3B, D). As for the inter-rhopaliar canals, the colouration is only present at the connection with the gastrovascular cavity, and generally fainter than those of the rhopaliar canals (Fig. 3A–C). In some specimens, the colouration and patterns can also be seen through the exumbrellar surface, which in fact are colour patterns and radiating markings of the radial canal on the subumbrella, appearing from apex towards the margin (Fig. 2A, B). Despite the intraspecific colour variation, *L. malayensis* is easily distinguishable from other *Lychnorhiza* species based on the whitish bell background and the distinctive colouration of radial canals (Table 2). It is noteworthy that all *L. malayensis* specimens (whether live or preserved) in the present study have colourless lappets, similar to the specimens collected from the Java Sea (Stiasny, 1920, 1921) and eastern India (Menon, 1930). Interestingly, images of *L. malayensis* specimens from southwestern India showed blue lappets (Jeyabaskaran et al., 2016), but there was no morphological description or voucher specimens for reference. Therefore we question their identification because blue-coloured lappet is a common feature for *L. lucerna* (Stiasny, 1921, 1932; Mianzan & Cornelius, 1999; Morandini, 2003).

Lychnorhiza malayensis is characterised as having eight velar lappets per octant (Stiasny, 1921, 1932; Kramp, 1961). This is true for all specimens in the present study, except in a mature individual (bell diameter 118 mm) from Klang Strait, which has seven to nine velar lappets per octant (Fig. 2C). Previously, variation in the number of velar lappets was detected among *L. malayensis* individuals found along the Indian coast, being eight or nine in number per octant (Menon, 1930; Table 1). Variation in the number of velar lappets was also reported for other members of the genus, and somehow overlapped with those described in *L. malayensis* (Table 2). For example, although *L. lucerna* was reported as having four velar lappets per octant, the number is possibly more in the larger or older specimen (Mianzan & Cornelius, 1999; Morandini, 2003). As for *Lychnorhiza* sp. aff. *L. lucerna*, the number of velar lappet per octant

can vary from four to eight in both adults and juveniles (Cedeño-Posso & Pérez, 2013). The oral arms in the current specimens are consistent in size (in proportion with bell diameter) but appear to be shorter and broader than those previously described for *L. malayensis*. We found the total length of the oral arms to be less than half of bell diameter, while the length of specimens from the Indian coasts and Java Sea ranged from $\frac{2}{3}$ of bell diameter (Menon, 1930) to as long as the bell diameter (Stiasny, 1921, 1932; Kramp, 1961). In our specimens, the length of the winged-portion of oral arms (i.e., half of total arm's length) also appear to be shorter than previous descriptions, which can reach up to $\frac{3}{4}$ of the total arm's length (Menon, 1930; Stiasny, 1932; see Fig. 4). The width of the winged-portion of oral arms appear relatively broader and laterally flattened than those found in the type specimen (Stiasny, 1921, 1932). Such discrepancies suggest intraspecific or inter-population variation of *L. malayensis* between geographic regions.

The variation among populations often represents phenotypic plasticity in response to variable environmental conditions, such as prey availability and water current (Dawson & Martin, 2001; Bolton & Graham, 2004; Dawson, 2005). However, the discrepancy of morphological features found in the present study and those in historical literature were accounted by the smaller sample sizes examined by the respective authors (see Table 1). Undoubtedly, the intraspecific variations and overlapping features confound the identification of jellyfish in general, and the application of molecular genetic techniques such as DNA sequencing and barcoding can facilitate species identification. Nevertheless, for some jellyfish species, their colour variants could not be genetically distinguished (Rizman-Idid et al., 2016). Although *L. malayensis* can be distinguished morphologically from its congeners, it is important that the full range of its intra-species variation be documented.

Relatedly, issues regarding the unavailability of *L. malayensis* type specimen and molecular identification need to be addressed for the benefit of future studies. Most taxonomical studies rely on type specimens as reference, or alternatively, specimens collected from the type locality, neither of which have been obtained here. Therefore, despite contributing additional knowledge towards *L. malayensis* taxonomy and its distribution, there are still uncertainties whether: (1) *L. malayensis* could still be found in the Java Sea since the last collection with proper identification from the area was done nearly a century ago; and (2) the specimens would be morphologically similar to those found in Malaysia. As for the application of DNA sequences to facilitate species identification, this can only be achieved if the known species has been barcoded previously. To date, GenBank has no COI gene sequences of *L. malayensis*. The only *Lychnorhiza* sequences available are of *L. lucerna* and some unidentified species from South and Central America (e.g., Gómez-Daglio & Dawson, 2017). Therefore, future studies should aim to barcode *L. malayensis* based on specimens from the type locality, providing sound reference sequences for future identification purposes.

Overall, our conclusions based on morphology are obvious and somewhat undeniable; the specimens from the coasts of Peninsular Malaysia are indeed *L. malayensis* as clearly shown by comparison with other *Lychnorhiza* species. Our results also agree with previous descriptions of *L. malayensis*. More broadly, future work should include more detailed morphological examination with greater geographical coverage and sample size, complemented with molecular genetic analysis for quantifying population differentiation in *L. malayensis*.

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LITERATURE CITED

- Appeltans W, Ah Yong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Blazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan T-Y, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, De Cock W, De Grave S, de Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Franssen, CHJM, Furuya H, Garcia-Alvarez, O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopperoff RR, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, Macpherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha RM, Saiz-Salinas JI, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Thuesen EV, Timm T, Todaro MA, Turon X, Tyler S, Uetz P, van der Land J, Vanhoorne B, vanOfwegen LP, van Soest WM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams GC, Wilson SP & Costello MJ (2012) The magnitude of global marine species diversity. *Current Biology*, 22(23): 2189–2202.
- Awong H, Ibrahim S, Ambak MA & Samo K (2010) Jellyfish (semi-china type) processing for human consumptions in Darvel Day, Sabah, Malaysia. *Borneo Research Journal*, 4(1): 59–70.
- Azila A & Chong VC (2010) Multispecies impingement in a tropical power plant, Straits of Malacca. *Marine Environmental Research*, 70(1): 13–25.
- Azila NA & Othman I (1993) Cases of jellyfish envenomization in Malaysia and some cytotoxic studies on their toxin. In: Tan NH, Oo SL, Thambyrajah V & Azila NA (eds.) *Proceedings: Advances in Venom and Toxin Research, Third Asia Pacific Congress on Animal, Plant and Microbial Toxins*. Malaysian Society on Toxinology, Kuala Lumpur. Pp. 113–118.
- Bolton T & Graham WM (2004) Morphological variation among populations of an invasive jellyfish. *Marine Ecology Progress Series*, 278: 125–139.
- Brotz L, Schiariti A, López-Martínez J, Álvarez-Tello J, Peggy Hsieh Y-H, Jones RP, Quiñones J, Dong Z, Morandini AC, Preciado M, Laaz E & Mianzan H (2017) Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Reviews in Fish Biology and Fisheries*, 27: 1–29.
- Cedeño-Posso C, & Pérez OPL (2013) Primer registro de medusas del género *Lychnorhiza* (Cnidaria: Scyphozoa: Rhizostomeae: Lychnorhizidae) en el Mar Caribe colombiano. *Boletín de Investigaciones Marinas y Costeras*, 42(2): 387–393.
- Clarke KR & Gorley RN (2006) *PRIMER V6: User Manual/Tutorial*. PRIMER-E Ltd., Plymouth, United Kingdom, 192 pp.
- Clarke KR & Warwick RM (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Second edition. PRIMER-E Ltd., Plymouth, United Kingdom, 256 pp.
- Cuvier G (1799) Sur l'organisation de l'animal nommé méduse. *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts*, 49: 436–440.
- Dawson MN (2005) Five new subspecies of *Mastigias* (Scyphozoa: Rhizostomeae: Mastigiidae) from marine lakes, Palau, Micronesia. *Journal of the Marine Biological Association of the United Kingdom*, 85(3): 679–694.
- Dawson MN & Martin LE (2001) Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semeaestomeae): some implications from molecular phylogenetics. *Hydrobiologia*, 451: 259–273.
- Department of Marine and Coastal Resources Thailand (2018) Central Database System and Data Standard for Marine and Coastal Resources. Department of Marine and Coastal Resources, Ministry of Natural Resources and Environment, Thailand. <http://marinegiscenter.dmcrc.go.th/km/jellyfish01/> (Accessed 2 August 2018).
- Goette A (1887) *Entwicklungsgeschichte der Aurelia aurita und Cotylorhiza tuberculata*. Leopold Voss, Hamburg & Leipzig, 79 pp.
- Gómez-Daglio L & Dawson MN (2017) Species richness of jellyfishes (Scyphozoa: Discomedusae) in the Tropical Eastern Pacific: missed taxa, molecules, and morphology match in a biodiversity hotspot. *Invertebrate Systematics*, 31(5): 635–663.
- Graham WM & Bayha KM (2008) Biological invasions by marine jellyfish. In: Nentwig W (ed.) *Biological Invasions*. Springer, Berlin, Heidelberg. Pp. 239–255.
- Graham WM, Pagès F & Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, 451: 199–212.
- Haeckel E (1880) *System der Acraspeden. Zweite Hälfte des Systems der Medusen. Acht Nachträge zur Vervollständigung des Systems*. Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena, 2: 361–672.
- Jeyabaskaran R, Mohan G, Abhilash KS, Prema D & Kripa V (2016) Is the Scyphozoan jellyfish *Lychnorhiza malayensis* symbiotically associated with the crucifix crab *Charybdis feriatus*? *Current Science*, 110(4): 479–480.
- Kramp PL (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom*, 40: 7–469.
- Light SF (1921) Further notes on Philippine scyphomedusan jellyfishes. *Ibid*, 18: 25–45.
- Menon MGK (1930) The Scyphomedusae of Madras and the neighbouring coast. *Bulletin of the Madras Government Museum*, 3: 1–28.

- Mianzan HW & Cornelius PFS (1999) Cubomedusae and Scyphomedusae. In: Boltovskoy D (ed.) South Atlantic Zooplankton. Backhuys Publishers, Leiden. Pp. 513–559.
- Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, 451: 55–68.
- Morandini AC (2003) Estrutura populacional de *Chrysaora lactea* e *Lychnorhiza lucerna* (Cnidaria, Scyphozoa) em amostras de plâncton, com a redescritção das espécies. Unpublished PhD Thesis, University of São Paulo, 133 pp.
- Morandini AC (2009) *Lychnorhiza lucerna* Haeckel, 1880 (Cnidaria, Scyphozoa, Rhizostomeae): Proposed conservation of generic and specific names (Case 3485). *Bulletin of Zoological Nomenclature*, 66(3): 133–138.
- Morandini AC, Martorelli SR, Marques AC & Silveira FL (2005) Digenean metacercaria (Trematoda, Digenea, Lepocreadiidae) parasitizing coelenterates (Cnidaria, Scyphozoa and Ctenophora) from Southeastern Brazil. *Brazilian Journal of Oceanography*, 53(1–2): 39–45.
- Mujiono N (2010) Jellyfish (*Crambionella* sp.) fisheries around Cilacap Waters, Central Java (Cnidaria: Scyphozoa). *Oceanologi dan Limnologi di Indonesia*, 36: 37–48.
- Nagata RM, Haddad MA & Nogueira Jr M (2009) The nuisance of medusae (Cnidaria, Medusozoa) to shrimp trawls in central part of southern Brazilian Bight, from the perspective of artisanal fishermen. *Pan-American Journal of Aquatic Sciences*, 4(3): 312–325.
- Nair KK (1951) Medusae of the Trivandrum coast. Part I. Systematics. *Bulletin of the Central Research Institute, University of Travancore, Series C, Natural Sciences*, 2: 47–75.
- Neethling S, Channing A, Gershwin LA & 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.
- Nicholas YWL & Yong OJ (2012) A survey of jellyfish (Cnidaria) around St John's Island in the Singapore Straits. *Contributions to Marine Science*, 2012: 57–74.
- Nishida S & Nishikawa J (2011) Biodiversity of marine zooplankton in Southeast Asia (Project-3: plankton group). In: Nishida S, Fortes MD & Miyazaki N (eds.) Coastal Marine Science in Southeast Asia – Synthesis Report of the Core University Program of the Japan Society for the Promotion of Science, 2001–2010, Coastal Marine Science. Terrapub, Tokyo. Pp. 59–71.
- Nishikawa J, Ohtsuka S, Mulyadi, Mujiono N, Lindsay D, Miyamoto H & Nishida S (2015) A new species of the commercially harvested jellyfish *Crambionella* (Scyphozoa) from central Java, Indonesia with remarks on the fisheries. *Journal of the Marine Biological Association of the United Kingdom*, 95(3): 471–481.
- Ohtsuka S, Kondo Y & Sakai Y (2010) In-situ observations of symbionts on medusae occurring in Japan, Thailand, Indonesia and Malaysia. *Hiroshima University General Museum Research Report*, 2: 9–18.
- Omori M & Nakano E (2001) Jellyfish fisheries in southeast Asia. *Hydrobiologia*, 451: 19–26.
- Petersen KW (1979) Development of coloniality in Hydrozoa. In: Larwood G & Rosen BR (eds.) *Biology and Systematics of Colonial Organisms*. Academic Press, London. Pp. 105–139.
- Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom*, 85(3): 461–476.
- Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science*, 4: 209–35.
- Purcell JE, Uye S & Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 350: 153–174.
- Richardson AJ, Bakun A, Hays GC & Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, 24(6): 312–322.
- Rizman-Idid M, Farrah-Azwa AB & Chong VC (2016) Preliminary taxonomic survey and molecular documentation of jellyfish species (Cnidaria: Scyphozoa and Cubozoa) in Malaysia. *Zoological Studies*, 55(35): 1–19.
- Rumpet R (1991) Some Aspects of the Biology and Fishery of Jellyfish found along the Coast of Sarawak, Malaysia. Department of Fisheries, Ministry of Agriculture, Kuala Lumpur, 53 pp.
- Schiariti A, Kawahara M, Uye S & Mianzan HW (2008) Life cycle of the jellyfish *Lychnorhiza lucerna* (Scyphozoa: Rhizostomeae). *Marine Biology*, 156(1): 1–12.
- Stiasny G (1920) Die Scyphomedusen-Sammlung des Naturhistorischen Reichsmuseums in Leiden: III. Rhizostomeae. *Zoologische Mededelingen*, 5(16): 213–230.
- Stiasny G (1921) Studien über Rhizostomeen mit besonderer Berücksichtigung der Fauna des Malaiischen Archipels nebst einer Revision des Systems. *Capita Zoologica*, 1(2): 1–179.
- Stiasny G (1932) IV—Ueber *Lychnorhiza malayensis* Stiasny. *Zoologische Mededelingen*, 15: 89–95.
- Verrill AE (1865) Classification of polyps (extract condensed from a Synopsis of the Polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). *Proceedings of the Essex Institute*, 4(1864–5): 145–152.
- von Lendenfeld R (1882) Über eine Übergangsform zwischen Semostomen und Rhizostomen (*Pseudorhiza aurosa*, g. & sp. n.). *Zoologische Anzeiger*, 5: 380–383.
- Williamson JA, Fenner PJ, Burnett JW & Rifkin JF (1996) *Venomous and Poisonous Marine Animals: A Medical and Biological Handbook*. Surf Life Saving Queensland Inc., University of New South Wales Press Ltd., Sydney, Brisbane, Queensland, 504 pp.
- WoRMS Editorial Board (2018) World Register of Marine Species. <http://www.marinespecies.org> (Accessed 26 October 2018).
- Yusoff FM, Nishikawa J & Kuppan P (2010) Commercial jellyfish, a little known fishery industry in Malaysia. *FishMail*, 18: 8–12.

APPENDIX

Appendix 1. List of morphometric, meristic and categorical morphological characters and states for *Lychnorhiza malayensis* and other *Lychnorhiza* species, adapted and modified from Gómez-Daglio & Dawson (2017).

f	Description	Character states
1	Bell diameter	millimetres
2	Mass of the whole medusae	grams
3	Umbrellar margin	smooth and continuous (no clefts, no lappets) = 0, clefts (or peronia) and lappets = 1
4	Number of velar lappets	count per octant
5	Number of bifurcated lappets	count per octant
6	Velar lappet length	millimetres
7	Velar lappet width	millimetres
8	Velar lappet shape	symmetric square = 1, symmetric semi-circular = 2, symmetric semi-oval = 3, symmetric tapering = 4, asymmetric square = 5, asymmetric semi-circular = 6, asymmetric semi-oval = 7, asymmetric tapering = 8
9	Velar lappets in heterogenous size classes	no = 0, yes = 1
10	Number of rhopaliar lappets	count per rhopalium
11	Rhopaliar lappet length (cleft depth)	millimetres
12	Rhopaliar lappet width	millimetres
13	Rhopaliar lappet shape	symmetric square = 1, symmetric semi-circular = 2, symmetric semi-oval = 3, symmetric tapering = 4, asymmetric square = 5, asymmetric semi-circular = 6, asymmetric semi-oval = 7, asymmetric tapering = 8
14	Rhopalia in marginal clefts	no = 0, yes = 1
15	Number of rhopalia	count per octant
16	Rhopalia position	perradial only = 0, interradial only = 1, adradial only = 2, perradial + interradial = 3, perradial + adradial = 4, interradial + adradial = 5, perradial + interradial + adradial = 6
17	Rhopalia location	at umbrellar margin = 0, distally on exumbrella = 2, median on subumbrella = 1, distally on subumbrella = 2
18	Circular muscle	well-developed = 0, marginal and tiny = 1
19	Number of circular muscle folds	count
20	Circular muscle covers radial septa or radial canal on proximal-distal axis	not at all = 0, partially = 1, exactly = 2, exceeds = 3
21	Circular muscle is continuous circularly over radial septae or radial canal	no = 0, yes = 1, mixed depending on position = 2
22	Radial muscles	absent = 0, weakly developed = 1, strongly developed = 2
23	Radial canals	absent = 0, present = 1
24	Circular canal	absent = 0, weakly developed chain of enlarged branches circumscribes bell = 1, a primary artery easily distinguishable from other canals circumscribes bell = 2
25	Number of perradial canal origins at the gastrovascular cavity	count per quadrant
26	Number of interradial canal origins at the gastrovascular cavity	count per quadrant
27	Number of adradial canal origins at the circular canal	count per quadrant

Appendix 1. Continued.

f	Description	Character states
28	Number of terminations of perradial canals at the circular canal	count per quadrant
29	Number of terminations of interradial canals at the circular canal	count per quadrant
30	Number of adradial-adradial anastomoses in radial canals that are circumscribed by the circular canal	count per quadrant
31	Number of perradial-adradial anastomoses in radial canals that are circumscribed by the circular canal	count per quadrant
32	Number of interradial-adradial anastomoses in radial canals that are circumscribed by the circular canal	count per quadrant
33	Number of blind terminations of adradial canals that are circumscribed by the circular canal	count per quadrant
34	Circular canal diameter	millimetres
35	Perradial diameter of the oral disc	millimetres
36	Interradial diameter of the oral disc	millimetres
37	Width of the oral pillars	millimetres
38	Depth of the oral pillars	millimetres
39	Number of subgenital ostium	count
40	Position of subgenital ostium	perradial only = 0, interradial only = 1, adradial only = 2, perradial + Interradial = 3, perradial + adradial = 4, interradial + adradial = 5, perradial + interradial + adradial = 6
41	Width of the subgenital ostium	millimetres
42	Height of the subgenital ostium	millimetres
43	Distribution of subumbrellar papilla within ostium	absent = 0, medial only = 1, peripheral only = 2, medial and peripheral = 3
44	Number of medial papilla	count per ostium
45	Number of peripheral papilla	count per ostium
46	Medial papilla width	millimetres
47	Medial papilla length	millimetres
48	Peripheral papilla width	millimetres
49	Peripheral papilla length	millimetres
50	Peripheral papilla length	millimetres
51	Medial papilla shape	ovoid = 0, oblong = 1, trapezoid = 2, hammer-like = 3, mixed = 4
52	Peripheral papilla shape	ovoid = 0, oblong = 1, trapezoid = 2, hammer-like = 3, mixed = 4
53	Shape of the gastrovascular cavity	circular = 0, cruciform = 1, pouched = 3, outfolded pockets = 4.
54	Perradial diameter of the gastrovascular cavity	millimetres
55	Interradial diameter of gastrovascular cavity	millimetres
56	Gastric filaments	absent = 0, present = 1
57	Number of gonads	count
58	Gonads are paired	no = 0, yes = 1

Appendix 1. Continued.

f	Description	Character states
59	Gonad position axis	perradial only = 0, interradial only = 1, adradial only = 2, perradial + interradial = 3, perradial + adradial = 4, interradial + adradial = 5, perradial + interradial + adradial = 6
60	Lateral distance from centre to most proximal portion of gonad	millimetres
61	Lateral distance from centre to most distal portion of gonad	millimetres
62	Gonad associated with particular structure	manubrium = 0, radial canals = 1, mesogleal protrusion (gastric septa or quadralinga) = 2, radial septa = 3, pouch = 4, out-folded pockets = 5
63	Structural form of gonad	digitate = 1, ribbon = 2, floret = 3
64	Manubrium	absent = 0, basal in arms = 1, basal and extended beyond arms = 2, pillars and disc = 3
65	Manubrium width at base	millimetres
66	Manubrium width at mouth	millimetres
67	Mouth lips	absent = 0, simple lips = 1, gelatinous or curtain-like arms = 2, oral arms with suckorial mouths = 3
68	Length of the proximal, unwinged portion of the oral arm	millimetres
69	Length of the distal, winged portion of the oral arm	millimetres
70	Oral arm width	millimetres
71	Cross-sectional form of oral arm	sheet-like = 1, two-winged = 2, three-winged = 3
72	Secondary structure of oral arm	absent = 0, spiral = 1
73	Fenestrations in oral arm	absent = 0, present = 1
74	Scapulae	absent = 0, present = 1
75	Terminal clubs on oral arms	absent = 0, present = 1
76	Distribution of intermediate filaments on the oral arm and oral disc	absent = 0, oral arm exterior only = 1, oral arm interior only = 2, oral disc only = 3, oral arm = 4, oral arm and disc = 5
77	Type of exumbrellar ornamentation	none (smooth) = 0, protuberance = 1, crenulation = 2
78	Colour of bell background	white = 0, light brown = 1, brown = 2, blue = 3, purple = 4
79	Colour of bell margin	no colour = 0, red = 1, brown = 2, reddish-brown = 3, blue = 4, purple = 5
80	Colour of markings on perradial canal	no colour = 0, light reddish-brown = 1, reddish-brown = 2, dark reddish-brown = 3, blue = 4, purple = 5
81	Colour of markings on interradial canal	no colour = 0, light reddish-brown = 1, reddish-brown = 2, dark reddish-brown = 3, blue = 4, purple = 5
82	Colour of markings on adradial canal	no colour = 0, light reddish-brown = 1, reddish-brown = 2, dark reddish-brown = 3, blue = 4, purple = 5
83	Distribution of colour patterns/markings on perradial canal	none (colourless) = 0, entire canal = 1, at the connection with circular canal = 2, at the connection with gastrovascular cavity = 3
84	Distribution of colour patterns/markings on interradial canal	none (colourless) = 0, entire canal = 1, at the connection with circular canal = 2, at the connection with gastrovascular cavity = 3
85	Distribution of colour patterns/markings on adradial canal	none (colourless) = 0, entire canal = 1, at the connection with circular canal = 2, at the connection with gastrovascular cavity = 3
86	Colour of oral arms	white = 0, light brown = 1, brown = 2, blue = 3, purple = 4
87	Colour of mouthlets/frills on oral arms	white = 0, light brown = 1, brown = 2, blue = 3, purple = 4

Appendix 1. Continued.

f	Description	Character states
88	Shape of markings on exumbrellar surface	none = 0, spot = 1, radiating line = 2, spot and radiating line = 3
89	Colour of markings on exumbrellar surface	no colour = 0, light reddish-brown = 1, reddish-brown = 2, dark reddish-brown = 3, blue = 4, purple = 5
90	Number of markings on exumbrellar surface	count per octant
91	Distribution of markings on exumbrellar surface	none (colourless) = 0, circular = 1, radiating toward bell margin = 2, circular and radiating toward bell margin = 3
92	Colour of gonads	white = 0, light brown = 1, brown = 2, blue = 3, purple = 4, green = 5

Appendix 2. List of images taken of preserved *Lychnorhiza malayensis* specimens, including the quantitative features emphasised in each image. The list was adapted and modified from the photography guideline for identification of scyphozoan jellyfish by Gómez-Daglio & Dawson (2017).

No.	Description
Tank	
1	Label (catalogue number)
2	Lateral view whole animal, camera in the front
3	Lateral view whole animal, camera in the front (include a colour chart)
4	Lateral view whole animal, camera at the side
5	Whole animal, camera from top (include a colour chart)
6	Close-up front/right quadrant, camera in the front or side
7	Close-up bell margin, camera in the front or side
8	Close-up of oral arms, camera in the front or side
9	Close-up of mouthlets, camera in the front or side
Position	Lift up bell/drape oral arms to expose ends of manubrium
10	Close-up of manubrium/mouth
11	Oral side up from top
Acrylic Stage	
Position	Subumbrella up (face up oral-aboral), tentacles/oral arms out Measure bell diameter _____ Measure oral disc diameter _____
12	Whole medusae, (include a colour chart) with flash
13	Whole medusae, bottom illuminated with black background
14	Whole medusae, full transillumination
Position	Move oral arms from quadrant
15	Close-up of quadrant, bottom illuminated with black background
16	Close-up of quadrant, no illumination with black background
17	Picture of centre, bottom illuminated with black background
18	Picture of centre, full transillumination
19	Close-up of velar lappets, bottom illuminated with black background
20	Close-up of velar lappets, full transillumination
21	Close-up of rhopalial lappets, bottom illuminated with black background
22	Close-up of rhopalial lappets, full transillumination
23	Close-up of rhopalium, bottom illuminated with black background
24	Close-up of rhopalium, full transillumination
25	Close-up of circular muscles, bottom illuminated with black background
26	Close-up of circular muscles, full transillumination
27	Close-up of gonad, bottom illuminated with black background
28	Close-up of gonad, full transillumination
29	Close-up of canals two quadrants, bottom illuminated with black background
30	Close-up of canals two quadrants, full transillumination
Position	Move oral arms to top in a group – reveal oral pillars
31	Close-up of oral pillar, bottom illuminated with black background
32	Close-up of oral pillar, full transillumination Measure depth of oral pillar _____ Measure height of oral pillar _____ Measure width of oral pillar _____
33	Close-up of subumbrellar papillae, bottom illuminated with black background
34	Close-up of subumbrellar papillae, full transillumination
Position	Splay half of oral arms out
35	Close-up of oral arms, bottom illuminated with black background
36	Close-up of oral arms, full transillumination
Position	Splay single oral arm out (winged portion), expose fenestrations (if any)
37	Close-up of single oral arm, bottom illuminated with black background
38	Close-up of single oral arm, full transillumination

No.	Description
Position	Flip animal so exumbrella faces up (face up oral-aboral)
39	Close-up of exumbrellar quadrant, bottom illuminated with black background
40	Close-up of exumbrellar quadrant, full transillumination
41	Whole animal exumbrella, bottom illuminated with black background
42	Whole animal exumbrella, full transillumination
Position	If dyeing canals possible – flip animal and dye canals
43	Close-up of dyed canals two quadrants, full transillumination
