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Panulirus stimpsoni and checklist of *Panulirus* lobsters in Malaysian waters: morphological and molecular insights

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Research Article

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Abstract

Panulirus stimpsoni is restricted to southern China, Vietnam, and Japan but has been rarely reported in tropical Gulf of Thailand. In Malaysia, only six species were previously reported. This study (1) reports the seventh Malaysian species – a new record of *P. stimpsoni* with morphological and genetic data; (2) establishes a checklist of Malaysian *Panulirus* species. Surveys from 2021 to 2022 sampled lobsters across Malaysia by SCUBA or from fishermen. Seven species were identified and a modified key of Malaysian species was constructed. The COI gene was used for genetic identification and phylogenetic tree reconstruction with maximum likelihood (ML). The best model was GTR + I + G. The ML tree comprised Clades I and II with sequences clustering by species and strong support. Most Peninsular Malaysian lobsters were *P. polyphagus* while *P. versicolor* dominated Sabah. Information on *P. stimpsoni's* full fishery potential, distribution, ecology, and biology is limited. Further research is needed to ensure conservation and management as data are only available for six previously reported species. Further studies are required to discover sustainable use approaches for all *Panulirus* species, particularly *P. stimpsoni*, given limited ecological understanding.

Introduction

Spiny lobsters under the genus of *Panulirus* exhibit a wide distribution and abundant presence in shallow tropical and subtropical waters, namely those with a depth of less than 100 m, in both the Northern and Southern hemispheres (Radhakrishnan *et al.*, 2019) and are observed across many types of substrates, including stony and coral structures. However, Lipcius *et al.* (2001) also noted that some lobsters were observed in marine environments at depths more than 100 m. Lobsters exhibit nocturnal behaviour and does not adhere to a certain dietary pattern and it is common for them to forage in sandy areas, where they can find a diverse range of food items (Chan, 1998; Childress and Jury, 2013; Senevirathna *et al.*, 2017; Setyanto *et al.*, 2019). Not only do they serve as crucial elements within marine ecosystems, fulfilling essential functions as both prey and predator, but they also represent one of the most significant fishery resources globally (Phillips, 2008). Nevertheless, there is a dearth of surveys undertaken in Malaysia, resulting in limited information regarding the range, variety, and population abundance of spiny lobster resources.

Previously, the Chinese spiny lobster, *Panulirus stimpsoni* (Holthuis, 1963), was restricted in the southern coast of China, including Hong Kong, and western coast of Taiwan (Holthuis, 1963, 1991), as well as northern coast of Vietnam (Gulf of Tonkin – An Luong edge), as the only temperate species in Vietnam (Nguyen and Nguyen, 2004). Previous records of *P. stimpsoni* were mostly in temperate water, as reported by Yoshimura *et al.* (2011), from western Kyusyu, Kanagawa, and Wakayama prefectures, and by Kim *et al.* (2009), from the Korean waters. Nonetheless, in 1991, Holthuis documented the first sighting of this species in the tropical environment of the Gulf of Thailand. This species inhabits reef areas at depth less than 40 m, with maximum body length around 16–23 cm and weight about 3 kg. The population size and distribution area of this species was reported to reduce rapidly since 1976 due to pollution, habitat loss, and overfishing. It has also been listed as an endangered species in the China Species Red List and the population is expected to decline further (Liu and Cui, 2011). Whilst, it was listed as Data Deficient in the International Union for Conservation of Nature (IUCN) Red List, last assessed date was in 2009 (Cockcroft *et al.*, 2009).

In Malaysia, only six species of spiny lobster were reported since 2004. *Panulirus ornatus* and *Panulirus polyphagus* were reported by Ikhwanuddin *et al.* (2014) and Halim and Siow (2019) in Peninsular Malaysia. Moreover, Waiho *et al.* (2021) studied the length–weight relationship and size at morphometric maturity of *Panulirus polyphagus* population from Johor Strait. In East Malaysia, three identified species (*P. ornatus, P. versicolor*, and *P. longipes*) were reported by Biusing and Chio (2004) in Sabah. Chen and Fatihah (2018) reported the

occurrence of *P. ornatus* and *P. versicolor* in Labuan. Moreover, the most recent finding was by Ng *et al.* (2022) and Ng *et al.* (2023), adding *P. femoristriga* and *P. h. homarus* to the list. Therefore, this study aims to (1) report a new record of spiny lobster species, *Panulirus stimpsoni*, with morphologic and molecular genetic information provided and (2) establish a checklist of *Panulirus* spp. spiny lobster in Malaysia waters.

Materials and methods

The surveys and sample collection pertaining to spiny lobsters were carried out in the waters of both East and Peninsular Malaysia. The observed and acquired *Panulirus* spp. are shown in Figure 1. A specimen of *Panulirus stimpsoni* was procured from a local fisherman in Pengerang, Johor, Malaysia, in February 2022. All collected specimens were transported to the laboratory for photographic documentation, including the frontal horn, sternum, lateral view of the abdomen, antennular plate, and ventral view of the antenna peduncle. The weight, total length (TL), carapace length (CL), and carapace width (CW) of all collected samples were all determined. Taxonomic criteria as presented in Chan (1998) were utilized for morphological species identification. An inventory of spiny lobsters (*Panulirus* spp.) was compiled for the waters of Malaysia. Furthermore, an amended key to the *Panulirus* spp. in Malaysia was developed in accordance with the study by Chan (1998).

For genetic identification, the abdominal tissue or antenna muscle of each specimen was dissected and fixed in ethanol for preservation (Ng *et al.*, 2023). Approximately 20 mg of preserved tissue was used for total genomic DNA extraction using the Toyobo MagExtractor-Genome-Kit. Universal primer pair LCO1490 + HCO2198 (Folmer *et al.*, 1994) were used in this study for the COI gene with sequence LCO1490: 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′ and HCO2198: 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′ of a 710 bp-fragment in *Panulirus* sp. lobster specimens. Gene amplification was performed using the protocol of the Vivantis *Taq* DNA Polymerase (recombinant) kit: 25-µl reaction containing 13.3 µl sterile distilled water, 2.5 µl ViBuffer A (10×), 2 µl dNTPs Mix (2.5 mM each), 1 µl $MgCl_2$ (50 mM), 2 µl of each primer (10 µM), 0.2 *Taq* polymerase (5 u μl^{-1}), and 2 µl DNA template with thermal cycle performed with initial denaturation at 94°C for 2 min, denaturation at 94°C for 30 s, followed by 30 cycles of annealing at 48°C for 30 s, and elongation at 72°C for 30 s, with an additional extension step of 7 min at 72°C. Amplicons were visualized on a 1.8% agarose gel. Purification of the amplicons was performed using Monarch PCR & DNA Cleanup Kit prior to DNA sequencing by 1st BASE DNA Sequencing Service using Sanger Sequencing. Then, the sequences obtained were uploaded to BLAST for preliminary identification of spiny lobster species.

The nucleotide sequences obtained were also used to reconstruct the phylogeny based on maximum likelihood (ML). The dataset comprised a total of 93 nucleotide sequences, including the *P. stimpsoni* specimens from Malaysian waters and other collected specimens from this study, as well as the closest outgroup species, *Parribacus antarcticus* Lund, 1793 (Decapoda, Scyllaridae). The outgroup was selected based on the molecular phylogenetic investigation of Palinuridae as described in Ravago and Juinio-Meñez (2003). The programme ClustalX (Thompson *et al.*, 2003) was used to multiple align the sequences and the Akaike Information Criterion (AIC) of jModelTest v.2.1.10 was used to evaluate and select an optimal evolutionary model (Darriba *et al.*, 2012). MEGA-X (Kumar *et al.*, 2018) was used to generate the ML tree (1000 bootstraps), as well as the intra- and inter-species *p*-distances. Further analyses were conducted to investigate the consistency between morphological characteristic (Michel, 1971; McWilliam, 1995; Lyons and Hunt, 1997; Sekiguchi and George, 2005; Matsuda *et al.*, 2006; Goldstein *et al.*, 2008; Froglia *et al.*, 2012; Konishi *et al.*, 2019) and the ML tree generated.

Results

Seven species of spiny lobster were identified from a total of 29 specimens collected in Malaysian waters: *P. stimpsoni* (2), *P. l. longipes* (9), *P. versicolor* (11), *P. polyphagus* (3), *P. femoristriga* (1), and *P. ornatus* (3). Table 1 contains an inventory of the species of spiny lobsters that have been identified in this study and in

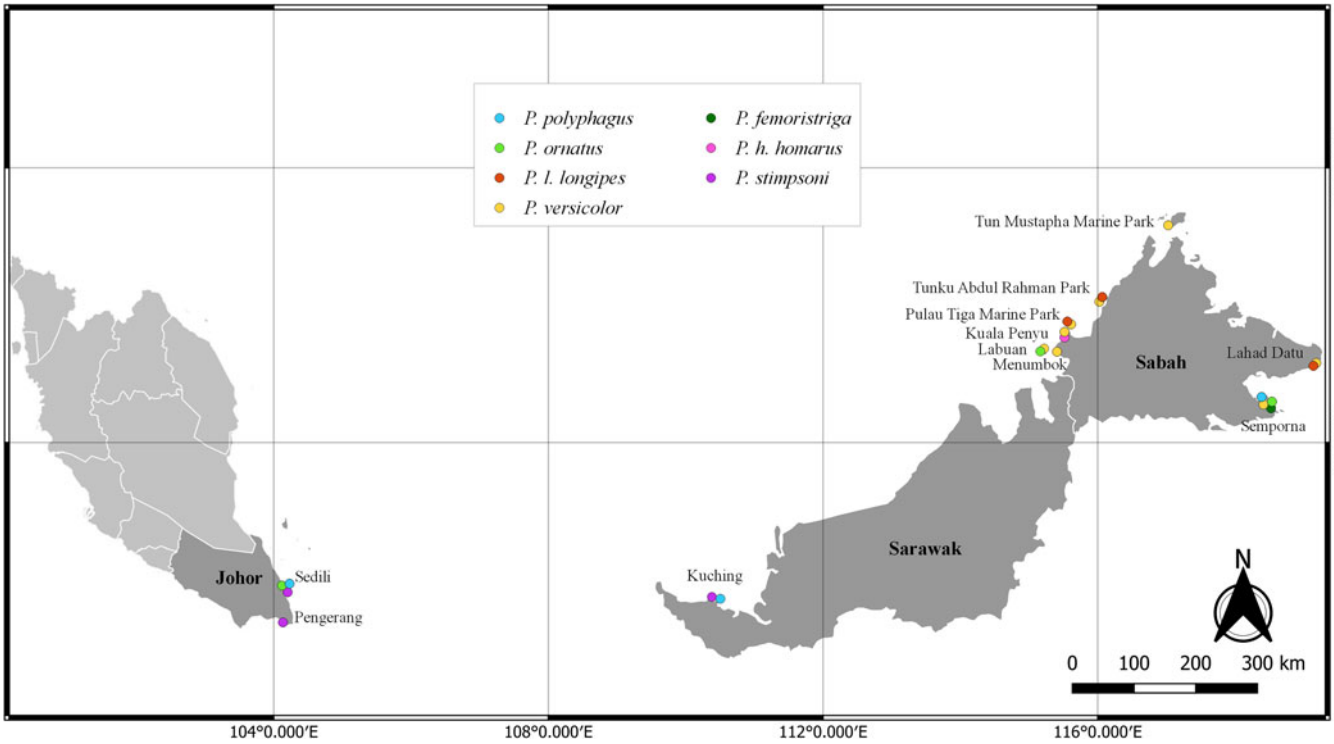

Figure 1. Map of Malaysia showing the location from which *Panulirus* spp. was obtained and sighted.

Table 1. Checklist of spiny lobster species identified in Malaysia waters

Species	Location	References
P. stimpsoni	Pengerang, Johor	Current study
	Kuching, Sarawak[a]	
P. ornatus	Semporna, Sabah	Current study
	Sedili, Johor	Halim and Siow (2019)
	Sabah	Biusing and Chio (2004)
	Labuan	Chen and Fatihah (2018)
P. versicolor	Pulau Tiga Park, Sabah	Current study
	Semporna, Sabah	
	Tunku Abdul Rahman Park, Sabah[a]	
	Menumbok, Sabah	
	Kuala Penyu, Sabah	
	Lahad Datu, Sabah	
	Tun Mustapha Park, Sabah	
	Sabah	Biusing and Chio (2004)
	Labuan	Chen and Fatihah (2018)
P. longipes longipes	Sabah	Biusing and Chio (2004)
	Pulau Tiga Park, Sabah	Current study
	Tunku Abdul Rahman Park, Sabah	
	Menumbok, Sabah	
	Lahad Datu, Sabah	
P. femoristriga	Semporna, Sabah	Ng *et al.* (2022)
P. polyphagus	Semporna, Sabah	Current study
	Pengerang, Johor	
	Sedili besar, Johor	
	Johor coastal waters	Ikhwanuddin *et al.* (2014)
P. homarus homarus	Kuala Penyu, Sabah	Ng *et al.* (2023)

[a]Sighted at the location but specimen not collected.

previous investigations. On the other hand, Table 2 contains the revised key to *Panulirus* spp. found in Malaysian waters. Each specimen collected for this study was accompanied by its weight, overall length (TL), carapace length (CL), abdomen width (AW), carapace width (CW), and total length (TL), which were all recorded. Using a representative specimen, the taxonomy of each identified species was described in this investigation.

Phylum ARTHROPODA Gravenhorst, 1843
Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Family PALINURIDAE Latreille, 1802
Genus *Panulirus* White, 1847
Panulirus stimpsoni Holthuis, 1963
Type locality: Hong Kong
Material Examine. One male: CL 81 mm, CW 63 mm, TL 196 mm, weight 386 g, February 2022, Pengerang, Johor, Malaysia (Figure 2).

Description

Rostrum absent; carapace rounded and spiny; anterior margin bearing irregular-sized spines other than frontal horns (Figure 3A). Antennules with flagella longer than peduncle; antennular plate at bases of antennae bearing two pairs of well separated principal spines (anterior pair considerably larger) (Figure 3C). First four pairs of legs without pincers. Thoracic sternum without submedian protrusion (Figure 3D). Each abdomen segments showed distinctive broad bands of setae (Figure 3B and 3E). Ventral surfaces of middle antennal segments with some scattered spinules (Figure 3F). Posterior half of tail fan soft and flexible. Colour: Body light green to light brown and covered with numerous white spots. Eyes black-brown. Eyestalks and frontal horn with bright orange reticulate markings. Antennular plate green; antennal flagella brownish and alternated with conspicuous white bands. Legs covered with prominent white spots. Abdomen covered with numerous small- to medium-sized white spots. Soft part of tail fan greenish-brown with posterior margin whitish. Pleopods greenish with white margins.

Panulirus ornatus (Fabricius, 1798)
Material examined. One female: CL 71.68 mm, CW 57.88 mm, TL 21.40 mm, weight 329 g, December 2021, Semporna, Sabah, Malaysia (Figure 4).

Description

Carapace rounded and spiny; rostrum absent; anterior margin bearing irregular-sized spines other than frontal horns (Figure 5A); antennules with flagella longer than peduncle;

Table 2. Keys to *P. stimpsoni* and other *Panulirus* spp. identified in Malaysia Waters (Modified from Chan, 1998)

No.	Descriptions	Species
1a.	Abdomen provided with transverse grooves	→ 2
1b.	Abdomen without transverse grooves or only with broad sunken pubescent areas.	→ 4
2a.	Anterior margins of transverse grooves on abdomen crenulated, grooves incomplete or interrupted in the middle; antennular plate bearing four well-separated principal spines and some small spinules; regions between eyestalks with bright orange and blue markings; legs blotched;	
	(i) body dark green to olive green; small squamae	*P. h. homarus*
	(ii) body brick red; large squamae	*P. h rubellus*[a]
2b.	Transverse grooves on abdomen with straight anterior margins, not crenulated; antennular plate with 2 principal spines; anterior margin of third abdominal pleuron not spinous; transverse groove of second abdominal segment joining corresponding pleural groove	→ 3
3a.	Median area at anterior carapace behind frontal horns usually bearing a longitudinal row of 3 spines only; ventral surfaces of distal 2 antennal segments each with 2 large spines only; thoracic sternum with 2 strong submedian protrusions; antennules with outer flagella dark brown and inner flagella entirely whitish; antennal peduncle including stridulating pad pinkish; lateral carapace with 2 complete longitudinal white strips extending along the entire carapace; legs striped	*Panulirus femoristriga*
3b.	Median area at anterior carapace behind frontal horns always bearing some smaller, irregular spines in addition to the regular row of 3 spines; ventral surfaces of distal 2 antennal segments each with 1 large spine (sometimes also with several other scattered spinules; thoracic sternum without strong submedian protrusions; antennules alternated with dark brown and white bands; antennular peduncle brown to purple and with stridulating pad bright blue; lateral carapace with 1 short (upper) and 1 long (lower) longitudinal white stripes; legs striped or spotted	*Panulirus longipes longipes*
4a.	Abdomen naked and smooth; legs blotched	→ 5
4b.	At least second and third abdominal segments with broad sunken pubescent areas	→ 6
5a.	Antennular plate armed with two pairs of principal spines; body greenish and abdomen with broad transverse dark bands, legs and antennules conspicuously ringed with light yellow and black	*Panulirus ornatus*
5b.	Antennular plate armed with one pair of principal spines; body pale green and abdomen with narrow transverse yellowish white bands	*Panulirus polyphagus*
6a.	Legs striped; antennular plate armed with 2 pairs of principal spines only; fourth to sixth abdominal segments smooth; body deep blue and green, abdomen with narrow transverse white bands, antennal and antennular flagella whitish	*Panulirus versicolor*
6b.	Legs blotched; antennular plate with many small spinules in addition to two pairs of principal spines; sunken pubescent areas present on all abdominal segments with distinctive broad bands of setae; body greenish, abdomen not banded and region between eye stalks not brightly marked but eyestalks and frontal horn with bright orange reticulate markings.	*Panulirus stimpsoni*

[a]Not found in Malaysia.

antennular plate at bases of antennae bearing two pairs of well separated principal spines (anterior pair considerably larger), sometimes also with several spinules (Figure 5C). First four pairs of legs without pincers. Thoracic sternum without submedian protrusions (Figure 5D). Abdomen naked and smooth, without transverse grooves or sunken pubescent areas (Figure 5B and 5E). Ventral surfaces of middle antennal segments with a row of two equal-sized large spines, distal segments with one small spine only (Figure 5F). Posterior half of tail fan soft and flexible. Colour: body greenish with carapace slightly bluish. Eyes black-brown. Frontal horns intricately banded with yellowish white and brown markings. Antennal peduncle bluish with stridulating pad somewhat pinkish. Antennules and legs conspicuously ringed with pale yellow and black. Abdomen covered with broad transverse dark bands over middle of each segment and bearing large pale yellowish spots near hinges. Pleopods yellowish.

Panulirus versicolor (Latreille, 1804)

Material examined. One female: CL 79.46 mm, CW 62.58 mm, TL 242.00 mm, weight 445 g, April 2022, Tunku Abdul Rahman Park, Sabah, Malaysia (Figure 6).

Description

Carapace rounded and spiny, rostrum absent; anterior margin bearing four large regularly spaced larged spines other than frontal horns (Figure 7A); abdomen more or less smooth, with broad but shallow sunken pubescent areas (Figure 7B and 7E); antennular plate at bases of antennae armed with two pairs of well-separated principal spines only (anterior pair larger) (Figure 7C); thoracic sternum without submedian protrusions (Figure 7D); ventral surfaces of distal two antennal segments flanked by some scattered spinules (Figure 7F);. first four pairs of legs without pincers. Posterior half of tail fan soft and flexible. Colour: body generally blue and green; more greenish in large individuals. Carapace, including frontal horns, with a mosaic pattern of green, white and blue. Eyes black-brown. Antenna with inner surface pink and outer surface blue; inner surface of antennular peduncle white,outer surface blue; flagella whitish. Legs blue, distinctly striped with white lines. Abdomen greenish, having white lines with blue margins along posterior margin of each segment. Soft part of tail fan green and blue. Pleopods blue, with white margins and a conspicuous medial white line.

Panulirus longipes longipes (A. Milne-Edwards, 1868)

Material examined. One female: CL 79.04 mm, CW 61.24 mm, TL 260.00 mm, weight 440 g, May 2022, Menumbok, Sabah, Malaysia (Figure 8).

Description

Carapace rounded and spiny; rostrum absent; anterior margin armed with irregular-sized spines; median area behind frontal horns always bearing some additional spinules other than the

Figure 2. A male specimen of *P. stimpsoni* (Holthuis, 1963) collected from Pengerang, Johor, Malaysia.

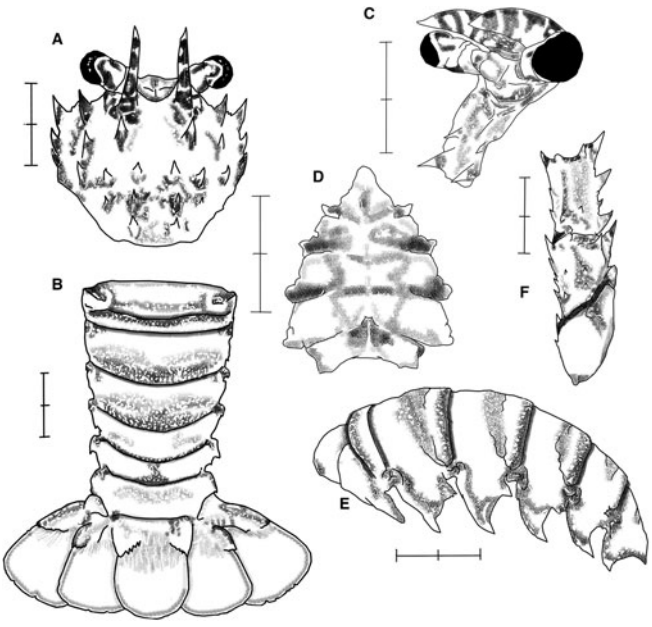

Figure 3. *P. stimpsoni* (Holthuis, 1963), Pengerang, Johor, Malaysia (male: A. Anterior carapace; B. Abdomen, dorsal view; C. Antennular plate; D. Thoracic sternum; E. Abdomen, lateral view; F. Antennal peduncle, ventral view. Scale bars, 20 mm).

regular longitudinal row of three spines (Figure 9A); abdominal segments with a complete transverse groove joining the pleural groove; abdominal pleura only with that of second segment sometimes bearing spinules (Figure 9B and 9E). Antennular plate at bases of antennae bearing one pair of well-separated principal

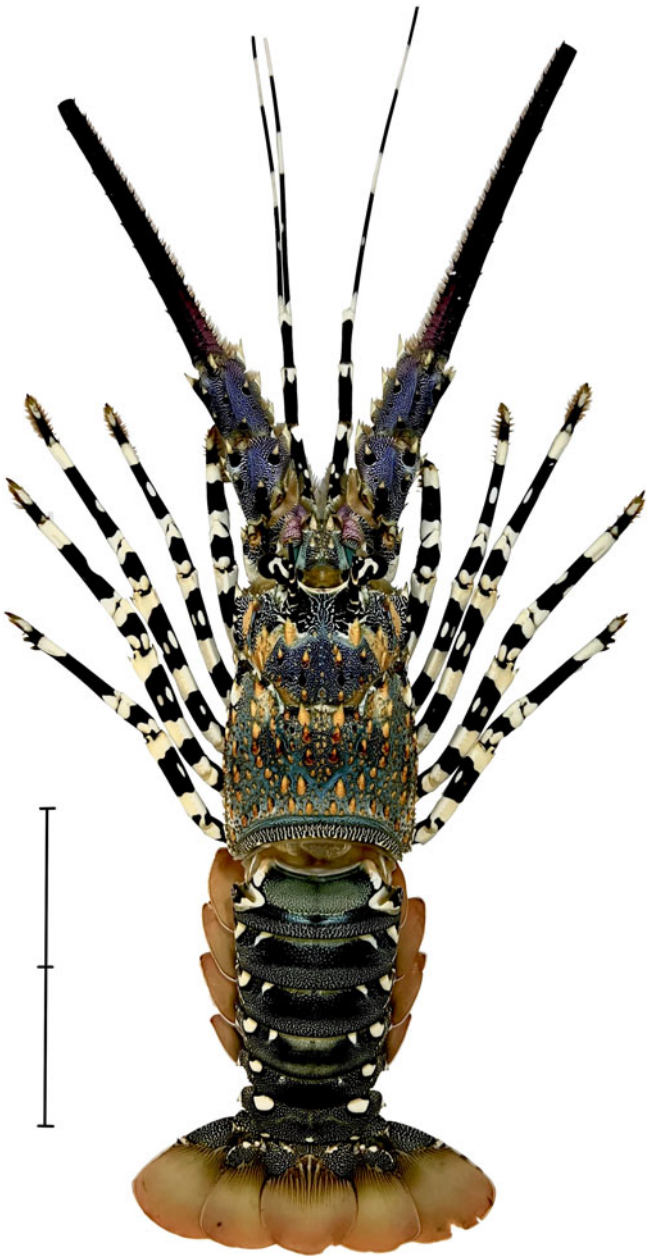

Figure 4. A female specimen of *P. ornatus* collected from Semporna, Sabah, Malaysia. Scale bar, 100 mm.

spines and some scattered spinules (Figure 9C); thoracic sternum without strong submedian protrusions (Figure 9D). Ventral surfaces of distal two antennal segments each with one large spine, often flanked by some scattered spinules (Figure 9F). First four pairs of legs without pincers. Posterior half of tail fan soft and flexible. Colour: body dark brown to indigo and covered with numerous white spots and markings. Eyes black-brown. Inner surfaces of antennae and antennular plate brown to purple and with stridulating pad bright blue; antennal flagella brownish with ventral surface lighter in colour; antennules dark brown and alternated with conspicuous white bands. Legs covered with prominent white spots connected by orange lines. Abdomen covered with numerous small- to medium-sized white spots. Soft part of tail fan orange-brown with posterior margin whitish. Pleopods somewhat greenish with white margins.

Panulirus polyphagus (Herbst, 1793)

Material examined. One female: CL 69.36 mm, CW 50.36 mm,

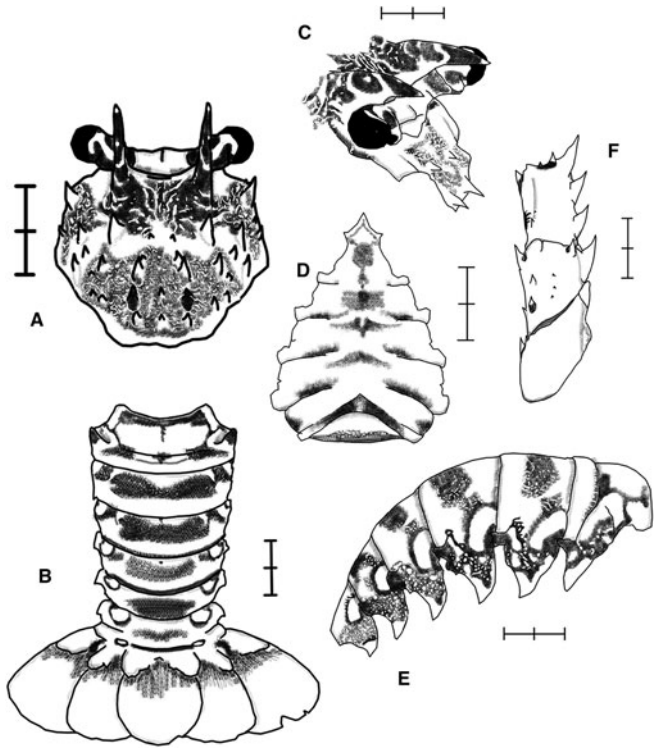

Figure 5. *P. ornatus* (Fabricius, 1798), Semporna, Sabah, Malaysia (female: A. Anterior carapace; B. Abdomen, dorsal view; C. Antennular plate; D. Thoracic sternum; E. Abdomen, lateral view; F. Antennal peduncle, ventral view. Scale bars, 20 mm).

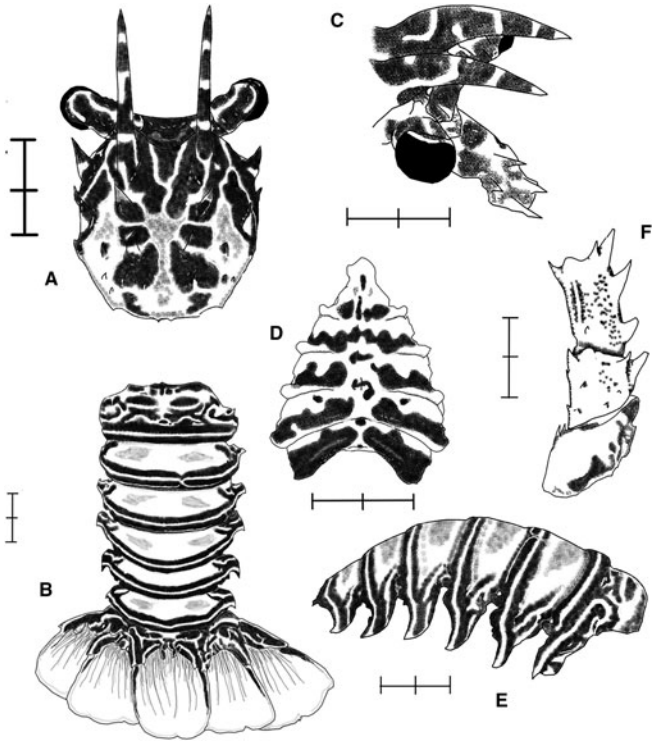

Figure 7. *P. versicolor* (Latreille, 1804), Tunku Abdul Rahman Park, Sabah (female: A. Anterior carapace; B. Abdomen, dorsal view; C. Antennular plate; D. Thoracic sternum; E. Abdomen, lateral view; F. Antennal peduncle, ventral view. Scale bars, 20 mm).

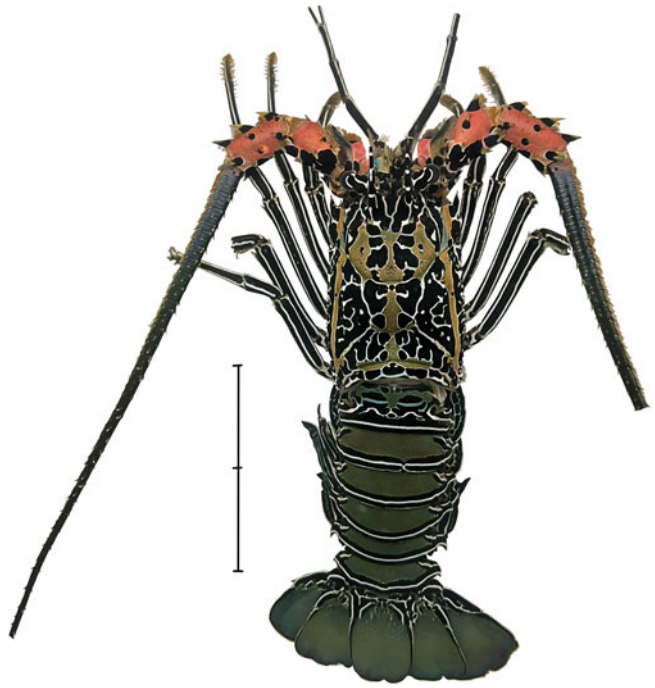

Figure 6. A female specimen of *P. versicolor* collected from Tunku Abdul Rahman Park, Sabah, Malaysia. Scale bar, 100 mm.

TL 198.00 mm, weight 238 g, December 2021, Semporna, Sabah, Malaysia (Figure 10).

Description

Carapace rounded and spiny; rostrum absent; anterior margin with irregular-sized spines other than frontal horns (Figure 11A); abdomen naked and smooth; without transverse grooves or sunken pubescent areas (Figure 11B and 11E). Antennular plate at bases of antennae armed with one pair of well-separated principal spines only (11c). Thoracic sternum without protrusions (Figure 11D). Ventral surfaces of distal two antennal segments without any spines or spinules (Figure 11F). Antennules with flagella longer than peduncle; first four pairs of legs without pincers. Posterior half of tail fan soft and flexible. Colour: body dull green; eyes black-brown; spines on carapace with yellowish brown tips, orbital margin and posterior marginal groove yellowish white; antennular plate with a medial longitudinal yellowish white line; antennular peduncle alternated with yellowish white and pale green bands, flagella banded with yellowish white and dark brown; legs light brown with yellowish white blotches; abdomen with tiny pale dots; a yellowish white band with brown margins near posterior border of each segment. Pleopods and soft part of tail fan orange-brown with yellowish white margins.

Panulirus femoristriga Von Martens, 1872
Panulirus longipes femoristriga von Martens, 1872
(original description)
Panulirus albiflagellum Chan et Chu, 1996 (junior synonym)

One female specimen was collected in this study from Semporna, Sabah, Malaysia in December 2021 with CL 56.32 mm, CW 45.50 mm, TL 196.00 mm and weight 186 g. Illustration and diagnosis information of this species is available in the study of Ng *et al.* (2022).

Panulirus homarus homarus (Linnaeus, 1758)

Current study did not obtain any specimen of this species. For more details of this species, please refer to Ng *et al.* (2023).

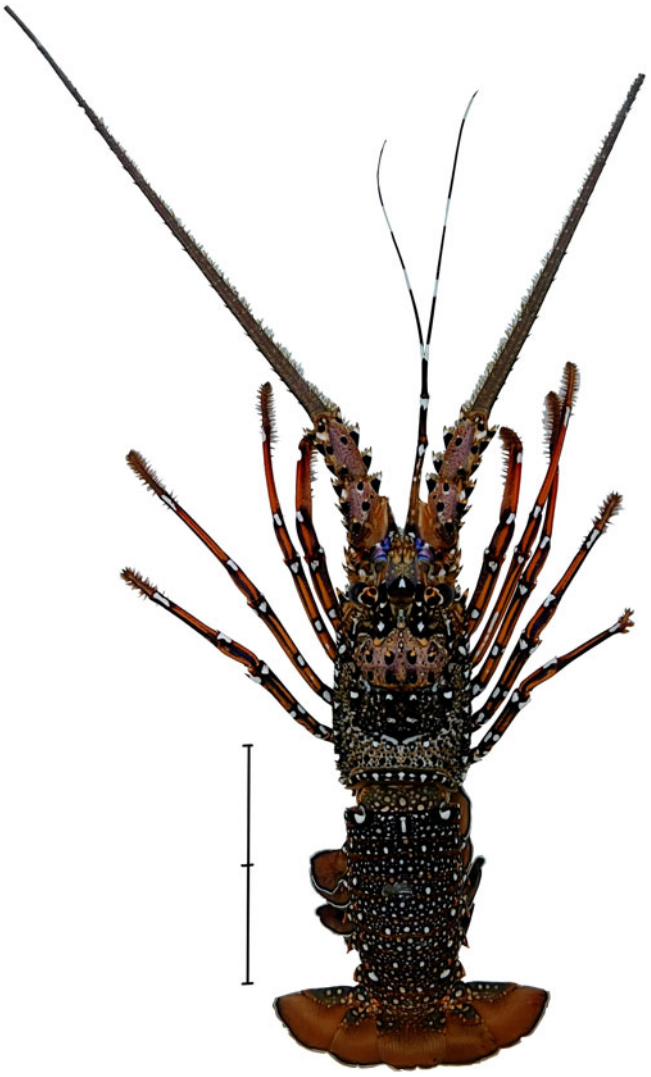

Figure 8. A female specimen of *P. longipes longipes* collected from Menumbok, Sabah, Malaysia. Scale bar, 100 mm.

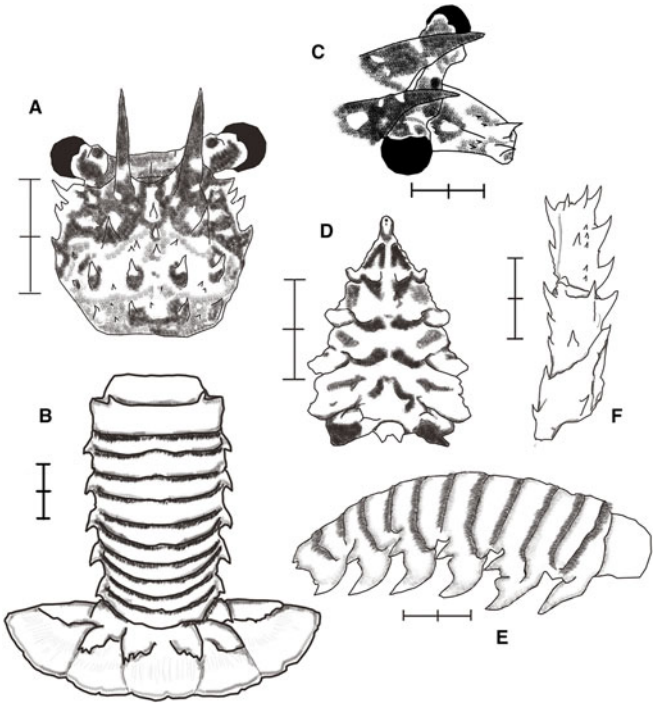

Figure 9. *P. longipes longipes* (A. Milne-Edwards, 1868), Menumbok, Sabah, Malaysia (Female: A. Anterior carapace; B. Abdomen, dorsal view; C. Antennular plate; D. Thoracic sternum; E. Abdomen, lateral view; F. Antennal peduncle, ventral view. Scale bars, 20 mm).

Phylogenetic analysis and sequence divergence

jModelTest was used to estimate the best model (based on corrected AIC; GTR + I + G model, General Time Reversible model with invariant sites and non-uniform evolutionary rates or gamma distribution) of the COI fragment dataset in this study selected with Overall, two major clades (Clade I and Clade II) were present in the COI ML tree as shown in Figure 12. *P. l. longipes*, and *P. femoristriga* were in Clade I while the other collected specimens were in Clade II. Each *Panulirus* spp. gathered in this study were grouped according to their species, with strong bootstrap value exceeding 99%. *P. stimpsoni* from present study (OR574256 and OR574267) were grouped together with *P. stimpsoni* (JN591365 and AF339471) from Hong Kong waters, with significant bootstrap value of 100%. It grouped as sister species with *P. versicolor* + *P. regius*, but with weak bootstrap value (< 50%, not shown in the tree). Similar results were observed in *P. ornatus* where it is grouped together with subspecies of *P. homarus* as sister species but with weak bootstrap value. The inter-species *p*-distance of each *Panulirus* sp. was more than 10% while intra-species *p*-distance less than 3%, thus, confirming the respective species. The *p*-distances within *P. stimpsoni* were 0.8–2.2%, while the *p*-distance of *P. stimpsoni* with molecular closely related species (*P. versicolor and P. regius*) was more than 10% (Table 3). For more phylogenetic information on *P. femoristriga* and *P. h. homarus*, refer to the study by Ng *et al.* (2022) and Ng *et al.* (2023), respectively. Sequence dataset in current study were also uploaded to GenBank, with the accession number: OR574256 – OR574284. The two *P. stimpsoni* specimens collected in this study have been deposited in Borneo Marine Research Institute collection with voucher number: IPMB-Cr 13.00001 and IPMB-Cr 13.00002.

Furthermore, Figure 12 demonstrated the clades' coherence with respect to morphological characteristics. While the exopod absent in Clade II species, it is present in the third maxilliped in Clade I species, either with or without a flagellum. While all *Panulirus* spp. possess an exopod on the second maxilliped, only Clade I species have flagellum, whereas Clade II species have either a reduced flagellum (*P. h. homarus*) or none at all (*P. versicolor*, *P. stimpsoni*, and *P. ornatus*). Clade I species were exclusively identified by the presence of transverse grooves on abdominal somites, whereas Clade II species exhibited a mixture of presence and absence of such grooves.

Discussion

This study provides the most recent and comprehensive survey of the *Panulirus* spp. that are currently known to exist in Malaysia. Seven species of spiny lobsters have been identified in the waters of Malaysia Sabah, situated in the Indo-Pacific Centre region renowned for its high biodiversity, generally harbours a more extensive assortment of spiny lobster species in comparison to Peninsular Malaysia. Thus, six species of spiny lobsters were identified in Sabah, and three were discovered in Johor, including the newly recorded *P. stimpsoni*. The morphological identification of every species obtained from the waters of Malaysia was precisely consistent with the descriptions found in previous works. Nevertheless, the visual resemblance between *P. femoristriga* and *P. longipes* renders it challenging to ascertain the exact species and worldwide distribution of these two species on account of the

Figure 10. A female specimen of *P. polyphagus* was collected from Semporna, Sabah, Malaysia. Scale bar, 100 mm.

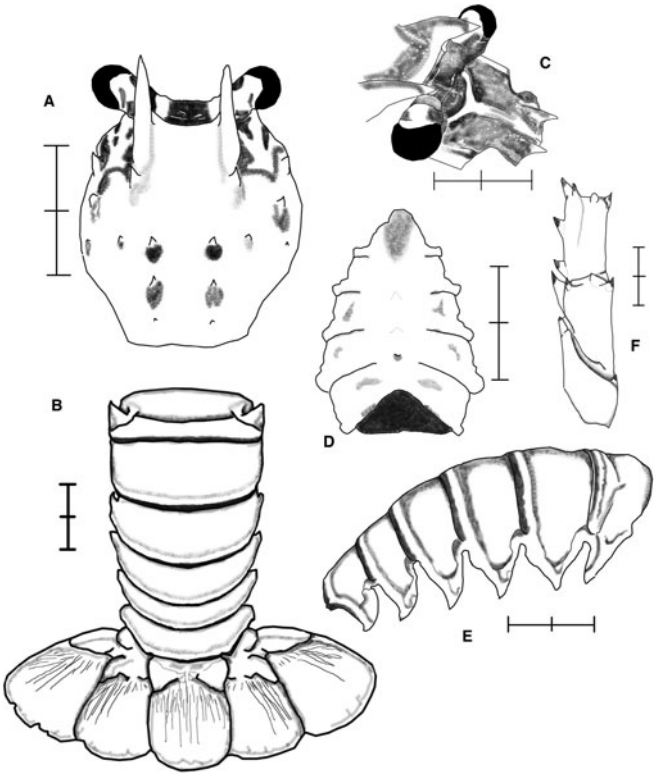

Figure 11. *P. polyphagus* (Herbst, 1793), Semporna, Sabah, Malaysia (Female: A. Anterior carapace, dorsal. B. Antennular plate, dorsolateral. C. Thoracic sternum, ventral. D. Thoracic sternum, ventral. E. Abdomen, right lateral. Scale bars, 20 mm).

scant data pertaining to the coloration of their flagella in past studies, as analysed in Ng *et al.* (2022). Legs patterned with prominent white lines and a white inner flagellum serve to validate the species identification of the *P. femoristriga* specimen described in Ng *et al.* (2022). To obtain further elucidation and elaboration, along with information regarding the worldwide distribution of this species, refer to the study by Ng *et al.* (2022).

A wide distribution was observed for *P. versicolor* and *P. longipes* across the Indo-West Pacific. The former species had a distribution that extended to regions including the Persian Gulf, Japan, Hawaii, the Red Sea, and Australia. Peninsular Malaysia had not documented *P. versicolor*, notwithstanding its wide-ranging distribution and classification as the most frequently observed species in Sabah and Labuan (Chen and Fatihah, 2018). The latter species, *P. longipes* comprises two officially recognized subspecies: *P. longipes longipes* and *P. longipes bispinosus*. The confirmation that all nine specimens of *P. longipes* used in this study are identified based on the observation having spotted legs, in contrast to the striped legs as observed on *P. l. bispinosus* (Chan and Ng, 2001; Sekiguchi and George, 2005). The range of this species expanded from Fiji to the eastern coast of Africa. Although both *P. versicolor* and *P. longipes* inhabit coral reef regions, their preferred depth of residence differs. Compared to the earlier species, which was typically observed at a maximum depth of 16 m in waters that are either clear or slightly turbid with strong currents, *P. longipes*, is typically found at depths of 130 m in waters that are either moderately turbid or clear (Holthuis, 1991).

Previously, only two species was documented from the waters of Peninsular Malaysia: *P. ornatus* and *P. polyphagus*, where only the former species was noted of their presence in both Peninsular and East Malaysia (Biusing and Chio, 2004; Ikhwanuddin *et al.*, 2014; Halim and Siow, 2019). The present study further established that *P. polyphagus* was present in the waters of Sabah. Both species are found in the Indo-West Pacific region. *P. ornatus* is known to inhabit East Africa and the Red Sea, whereas *P. polyphagus* is found in Thailand, Vietnam, Pakistan, the Philippines, India, Papua New Guinea, and northern Australia (Holthuis, 1991). Similar to other species, *P. ornatus* inhabits estuarine habitats, shallow areas of coral rubbles, and limestone pavement. It typically occurs at depths between 1 and 10 m. In contrast, *P. polyphagus* prefers muddy or rocky bottoms in turbid waters near river mouths at depths between 3 and 90 m. The elevated concentration of *P. polyphagus*, along with other spiny lobster species, likely signifies elevated turbidity in the waters of Johor, which can be attributed to the substantial sediment deposition caused by coastal development and industrial expansion (Misbari and Hashim, 2023).

Despite the extensive distribution of *P. h. homarus* throughout the Indo-West Pacific region (Holthuis, 1991), Ng *et al.* (2023) documented the first record of the species in the biodiversity database of Malaysia. The acquisition of a single specimen throughout the course of the research suggests that the population may be severely scarce in the wild. Nonetheless, this is also likely due to the fact that their preferred habitat is turbid water at a depth of 1–5 m, which restricts the spotting during SCUBA dives.

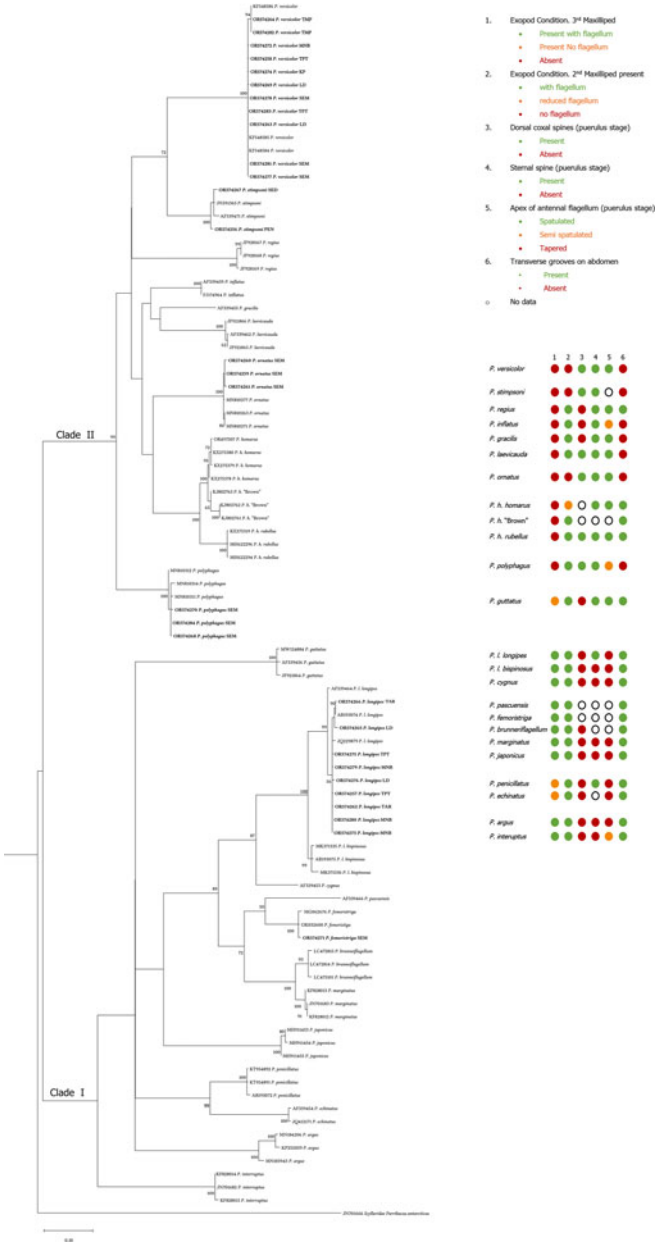

Figure 12. Maximum likelihood (ML) tree inferred from 93 partial mitochondrial COI sequences of *Panulirus* spp., with *Parribacus antarcticus* as outgroup. Values of the nodes correspond to bootstrap values, only values >50 are shown.

Furthermore, their pigmentation is strikingly comparable to that of *P. ornatus*; however, it is more subdued and lacks contrast. As a result, fishermen misidentify *P. h. homarus* as *P. ornatus*, assuming that its coloration renders it less valuable; consequently, they retain it for personal consumption, thereby limiting its availability on the market.

Conversely, information regarding the distribution of *P. stimpsoni* is limited; however, George and Main (1967) suggest that it was restricted to the waters of Hong Kong. Subsequently, Holthuis (1991) documented an uncommon sighting of this species in the Gulf of Thailand. Nguyen and Nguyen (2004) then reported on this species in the waters of Vietnam, noting that it is the only temperate species in the country. Nevertheless, similar to the Gulf of Thailand, tropical waters in Malaysia were also inhabited by *P. stimpsoni*. In addition to two specimens being purchased from Johor, where the fishermen claimed to have captured the species in Johor water, two specimens have also been observed in a market of Kuching, Sarawak, Malaysia. This observation may indicate that the distribution of *P. stimpsoni* is more extensive than is presently recognized in scientific knowledge (it has since expanded to lower latitudes in the hemisphere and is no longer restricted to the waters of Hong Kong). Additional research is necessary to verify the hypotheses regarding the species' abundance and distribution.

DNA barcodes are useful for species identification of lobsters and even DNA of larvae can be used to match with adult sequences for species confirmation as Chow *et al.* (2006), Palero *et al.* (2014), and Konishi *et al.* (2019) have successfully delimited phyllosoma larvae by employing COI barcode technique and Govender *et al.* (2019) also have consistent results with the adult specimen. Furthermore, this technique has been applied in other lobsters such as slipper lobsters of the genus *Acantharctus, Biarctus* (Genis-Armero *et al.*, 2023) *Chelarctus* (Ueda *et al.*, 2021) and *Scyllarides* (Hidaka *et al.*, 2022). Therefore, molecular phylogeny is an alternative way for species identification as it avoids possible misidentification and further verifies the identity of a specimen. Strong support has been provided by Ravago and Juinio-Meñez (2003) by using the mitochondrial DNA (mtDNA) COI sequences to distinguish the genetic variability between the 'banded whisker' and 'white whisker' of *P. longipes femoristriga*. The result of their phylogenetic analysis not only showed the distinction of *P. femoristriga* from *P. l. bispinosus*, but also clarified the phylogenetic relationships amongst the closely related species, such as *P. longipes longipes* and *P. longipes bispinosus*. On the contrary, Lavery *et al.* (2014) studied four subspecies of *P. homarus* and revealed that, *P. homarus megasculpta* and *P. homarus homarus* are genetically indistinguishable; *P. homarus* 'Brown' diverged much lesser degree than *P. h. rubellus* lineage, leaving its taxonomic status unclear. Similar results were obtained in the study by Ng *et al.* (2023). Thus, the only two subspecies currently recognized are *P. homarus homarus* and *P. homarus rebellus* (Radhakrishnan *et al.*, 2019).

The COI phylogenetic tree in this study showed that the collected specimens confirm to be the respective species as they were grouped together with low sequence divergence (<3%), thus validating the species collected in this study. *P. femoristriga* and *P. longipes longipes* were in Clade I while *P. stimpsoni, P. polyphagus, P. homarus, P. ornatus,* and *P. versicolor* were in Clade II. *Panulirus* spp. in Clade II showed significant difference in morphology particularly in colour and pattern on the exoskeleton: *P. stimpsoni* (light green to light brown) *P. polyphagus* (dull green), *P. homarus* (greenish to brownish), *P. ornatus* is slightly bluish, and *P. versicolor* is green. In addition, abdominal segments of these *Panulirus* spp. were also significantly different: *P. versicolor* (broad but sunken pubescent area), *P. homarus* (slightly crenated transverse grooves), *P. ornatus* and *P. polyphagus* (naked and smooth abdominal segments but the latter species has brown margins with a yellowish white band near the posterior border of each segment while in the middle of each segment of the former species is covered with broad transverse dark bands), and *P. stimpsoni* (distinctive broad bands of setae on each abdomen segments).

Despite the distinct morphology, these five species were all grouped under Clade II and similar findings was observed in the study carried by George and Main (1967). George and Main (1967) categorized the clade into two groups according to the degree of maxilliped modification: Group III (*P. polyphagus, P. regius, P. laevicauda, P. inflatus*) and Group IV (*P. stimpsoni, P. homarus, P. ornatus*, and *P. versicolor*). However, *P. polyphagus* was later transferred to Group IV as they possess dorsal coxal spines and a wide cephalic shield at phyllosoma stage, unlike *P. regius*, which has no dorsal coxal spines and a narrower cephalic shield (McWilliam, 1995). Group IV species are considered to be

Table 3. Number of sequences, *n*, and pairwise *p*-distance sequence divergence of *Panulirus* spp. collected in this study and their closely related species

	P. stimpsoni	*P. femorostriga*	*P.ornatus*	*P. polyphagus*	*P. h. homarus*	*P. l. longipes*	*P. versicolor*
P. stimpsoni	0.0088–0.0220						
	n = 12						
P. femorostriga	0.2181–0.2269	0.0066–0.0110					
	n = 12	*n* = 6					
P.ornatus	0.1454–0.1564	0.2247–0.2357	0.0000–0.0088				
	n = 24	*n* = 18	*n* = 30				
P. polyphagus	0.1366–0.1520	0.2070–0.2181	0.1608–0.1718	0.0022–0.0132			
	n = 24	*n* = 18	*n* = 36	*n* = 30			
P. h. homarus	0.1432–0.1608	0.2070–0.2159	0.1343–0.1432	0.1498–0.1630	0.0022–0.0066		
	n = 16	*n* = 12	*n* = 24	*n* = 24	*n* = 12		
P. l. longipes	0.2115–0.2269	0.1476–0.1586	0.2269–0.2379	0.2049–0.2181	0.2070–0.2159	0.0000–0.0242	
	n = 48	*n* = 36	*n* = 72	*n* = 72	*n* = 48	*n* = 132	
P. versicolor	0.1300–0.1410	0.2203–0.2291	0.1674–0.1762	0.1564–0.1652	0.1542–0.1608	0.2225–0.2335	0.0000–0.0088
	n = 56	*n* = 42	*n* = 84	*n* = 84	*n* = 56	*n* = 168	*n* = 182

the most derived (George and Main, 1967), thus, are expected to exhibit close genetic affinities but the topology of species within this Clade has not been resolved (Ravago and Juinio-Meñez, 2003). Resolving the topology of species within this Clade is not an objective of present study, yet, further study is recommended to allow better insight on the topography of this clade.

Moreover, no genetic boundary was detected among these species of *Panulirus* lobster in this study. Similar to the study of Halim *et al.* (2021), the DNA barcode of tiger prawn collected from Borneo and East coast of Peninsula Malaysia are in the same molecular clade. Nonetheless, they discovered that the tiger prawn from the west coast of Peninsular are of different lineage. Unfortunately, current study has not obtained any spiny lobster sample from this part of Malaysia to investigate whether if this also applies to spiny lobster. Further sampling effort within a narrower geographical scale is encouraged as it permitted a precise locality of the genetic break for this species within the Indo-Pacific Ocean. Although, previous study by Permana *et al.* (2019) ascertains that *P.ornatus* has two lineages in Indonesia and a 3rd lineage from Sri Lanka and Australia, yet, the sequences from Sri Lanka and Australia used in their phylogenetic tree of *P. ornatus* were actually the same sequence with GenBank accession number, AF339467, originated in Torres Strait, Australia (not Sri Lanka), by Ptacek *et al.* (2001). This sequence was employed in the present study previously to construct a COI phylogenetic tree and found that the dissimilarity within *P. ornatus* were >5%, which is congruent with the results in the study by Permana *et al.* (2019). However, intra-species *p*-distance within the *Panulirus* spp. was to be below 3%. Therefore, another COI phylogenetic tree (current) was re-constructed using sequences of Nguyễn *et al.* (2019) from Sri Lanka, Australia, and Vietnam (GenBank accession number: MN810271, MN810277, and MN810263, respectively) to ascertain whether *P. ornatus* has two or more lineages. Results reveal that these *P. ornatus* from Australia, Sri Lanka, Vietnam, Malaysia (present study) were from the same lineage with *p*-distance lower than 3%. This provides evidence that the COI sequence from Australia (AF339467) is incorrect, may be a nuclear pseudogene (or numt), as has been reported from other decapods COI sequences (Buhay, 2009). Similar results were reported by Lavery *et al.* (2014) regarding the sequence (GenBank accession AF339457) and by Ptacek *et al.* (2001).

Conclusion

In Malaysian waters, seven *Panulirus* spp. were discovered, of which *P. stimpsoni* was identified for the first time. Research on this species is limited, specifically regarding its distribution, despite the fact that it was formerly thought to be endemic to the waters of Hong Kong, shifted to a temperate species status, and is now documented in tropical countries like Malaysia. It has likely been disseminated to neighbouring tropical countries; therefore, additional research is necessary to determine the species' actual distribution and abundance. Conversely, in Peninsular Malaysia, the majority of spiny lobsters were found in Johor, where *P. polyphagus* dominated and *P. ornatus* comprised the minority. In Sabah, *P. versicolor* is the species that is most commonly observed, followed by *P. longipes* as the second most frequently observed species.

The recent discovery enhances the inventories of marine biodiversity in the Malaysian seas. Obtaining additional knowledge regarding marine biodiversity is intrinsically linked to the determination to safeguard the world's natural treasures, especially marine life. Given the fact that spiny lobsters are species of interest to the fishing industry, acquiring biological knowledge is vital for their sustainable fisheries management. Additionally, due to its high value on international markets, spiny lobsters are actively exploited and is under intense pressure due to the inadequate enforcement of fishery and marketing regulations. Consequently, additional research into *Panulirus* spp. is necessary in the future to identify methods for ensuring its sustainable management and utilization.

Data. The two *P. stimpsoni* specimens collected in this study have been deposited in Borneo Marine Research Institute collection with voucher number: IPMB-Cr 13.00001 and IPMB-Cr 13.00002. Sequence dataset in the current study were also uploaded to GenBank, with accession numbers: OR574256–OR574284.

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original draft, visualization. **RBN:** Investigation. **TST, CTY, LCP:** Formal analysis, validation. All authors have read and approved the final manuscript for publication.

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