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Phenotypic variation of *Thenus* spp. (Decapoda, Scyllaridae) in the waters of southern Thailand and Malaysia using multivariate morphometric analysis

Ihsan Hani Radzi[1,2], Cheng-Ann Chen[1*], Sukree Hajisamae[2], Kay Khine Soe[2]

[1] Borneo Marine Research Institute – Universiti Malaysia Sabah (88400, Kota Kinabalu – Sabah – Malaysia).
[2] Faculty of Science and Technology – Prince of Songkla University(94000, Pattani – Thailand).

* Corresponding author: chengann@ums.edu.my

ABSTRACT

Thenus spp. are slipper lobsters which are commercially significant as a food source with good aquaculture potential. This study focuses on collecting population information on *Thenus orientalis* and *Thenus indicus* from selected sites in southern Thailand and Malaysia to inform sustainable fisheries management about the resources. Twenty-five size-adjusted morphometric measurements were analyzed using canonical discriminant function and dendrogram cluster analyses to examine patterns of phenotypic variation between sites. Significant phenotypic variation with distinct centroids and minimal overlapping cases were observed among four sites of *T. orientalis* ($p < 0.05$), as well as cluster analysis groupings occurring as in (i) Kota Kinabalu and Kudat, in Sabah, Malaysia; (ii) Pattani; and (iii) Nakhon Si Thammarat, in Thailand, which were best discriminated by the width of the third pereiopod merus, the sixth abdomen segment, and the carapace posterior margin. Similar morphometric data between Kota Kinabalu and Kudat suggests a subpopulation of *T. orientalis* occurring in Sabah waters. Significant phenotypic variation was also detected between six sites of *T. indicus* ($p < 0.05$), with close centroids and overlapping cases forming three groups: (i) Ranong and Nakhon Si Thammarat; (ii) Kota Kinabalu, Tanjung Sedili, and Kuala Terengganu; and (iii) Pattani, best described by the widths of the second antenna and the first pereiopod merus, in addition to the length of the sixth abdomen segment. Cluster analysis shows the Pattani specimens clustering with the Malaysian specimens rather than the Thai specimens, suggesting homogeneous morphometric data between contiguous sites. Nakhon and Pattani forming separate groups in both species suggest discreet subpopulations occurring in the lower Gulf of Thailand. Patterns of phenotypic variation observed may be attributable to environmental conditions, local adaptations, and nomadic behavior. The findings can serve as baseline information for spatial planning in fisheries management, as well as to apprise regional efforts in the sustainable exploitation of *Thenus* spp.

Keywords: Flathead lobster, Discriminant function, Cluster analysis, Fisheries management

INTRODUCTION

Thenus Leach, 1816 is made up of five species that are commercially valuable as food and popular in a variety of cuisines. *Thenus* spp., commonly known as flathead lobsters, are among the edible species in the slipper lobster family Scyllaridae Latreille, 1825 due to their larger size compared to other scyllarids (Holthius, 1991). They are the few scyllarids with full aquaculture because of their relatively short life cycle, quick growth, resilient larvae, and non-aggressive behavior in culture settings (Rogers et al., 2010). There has been

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success in *Thenus* spp. aquaculture at experimental levels in Australia (Mikami and Kuballa, 2004) and India (Kizkhakudan et al., 2004). Recently, the Aquaculture Department of the Southeast Asian Fisheries Development Centre (AQD SEAFDEC) has begun developing an aquaculture program for *T. orientalis* in tropical conditions, achieving the notable milestone of spawning and egg-hatching in captivity (SEAFDEC, 2022). It is predicted that once commercial aquaculture is formed, *Thenus* aquaculture output will be a valuable source of food and income (Jeffs et al., 2020).

Thenus spp. are typically landed as bycatch of trawl fisheries. Currently, data on the wild populations of *Thenus* are scarce, despite continuous exploitation. The International Union for Conservation of Nature (IUCN) Red List categorizes members of this genus as “data deficient” indicating a dearth of data on *Thenus* spp. population status, distribution, and trends, as well as habitat and threats (IUCN, 2023). While large-scale aquaculture remains under development, the wild population continues to be exploited incidentally as the sole source of flathead lobsters for commercial purposes. This continuous exploitation, without comprehensive data, could be detrimental to their survival. For example, overexploitation led to a collapse of the *T. orientalis* population in Mumbai, India which has yet to recover (Jeena et al., 2019). Therefore, it is crucial to collect data on wild *Thenus* populations to inform fisheries management plans for the sustainable exploitation of this resource.

Phenotypic variation is often used to describe populations in a distribution range of commercial species (Chandran et al., 2022). Multivariate analyses of morphometric characters are consistently used to study the stocks of exploited crustacean species (Chybowski, 2014; Jónsdóttir et al., 2016; Du et al., 2022). Discriminant function and cluster analyses are prevalent techniques to detect phenotypic variation, since their results can be foundational data for characterizing populations and their interconnectivity (García-Dávila et al., 2005; Siddik et al., 2016). This study employed multivariate methods to investigate phenotypic variation in *Thenus* spp. present in the waters of Malaysia and southern Thailand to provide population information to support fisheries management within the region.

Disparities in scyllarid body forms have often been attributed to environmental factors and behavioral adaptations for habitat exploitation (Jones, 2007; Spanier et al., 2010). It would be informative to see how the species differ now, since studies indicate different preferences in water depth and sediment composition for each species (Jones, 1993, 2007; Iamsuwansuk et al., 2012). Phenotypic variation between sites is analyzed to identify discrete populations within the region. Phenotypic variation can be an indicator for discrete populations, which is useful to distinguish conservation units and to plan fisheries management systems (Zhang et al., 2016; Jawad et al., 2021).

Thus, this study aims to determine the pattern of phenotypic variation between selected sites for *T. orientalis* and *T. indicus*, respectively. This endeavor is a suitable first step in researching Malaysia’s unknown *Thenus* spp. population and it is beneficial in updating information on the *Thenus* spp. present in southern Thailand. Furthermore, we can determine whether fisheries management of *Thenus* spp. can be incorporated as a regional effort between these neighboring countries.

METHODS

Sample collection

Dead specimens of *Thenus* spp. that were entirely frozen in ice were collected from seven commercial lobster landing sites in Malaysia and southern Thailand (Figure 1). The sampling locations in Malaysia were divided into two main regions: Kota Kinabalu (KK) and Kudat (KD), representing East Malaysia on the Borneo Island, while Kuala Terengganu (KT) and Tanjung Sedili (TS) representing the Peninsular Malaysia. Meanwhile, the sampling locations in southern Thailand were Pattani (PT) and Nakhon Si Thammarat (NK), located on the Gulf of Thailand, and Ranong (RN), on the Andaman Sea side.

Morphological examination and morphometric measurements

Each specimen was physically examined to distinguish the morphological characteristics as described in the identification key provided by Burton and Davie (2007). Male and female specimens were differentiated macroscopically according to their sexual dimorphic characteristics, based on the position of gonophores at the third pereiopods for females and the fifth pereiopods for males (Alborés et al., 2019). Each individual was weighed, labelled, and photographed. Total length in addition to twenty-five other morphometric measurements of the body, carapace (dorsally measured), antennae, the propodus and merus of the first three pereiopods, two abdomen segments (dorsally measured), and telson of each specimen were taken using Vernier calipers (Figure 2, Table 1).

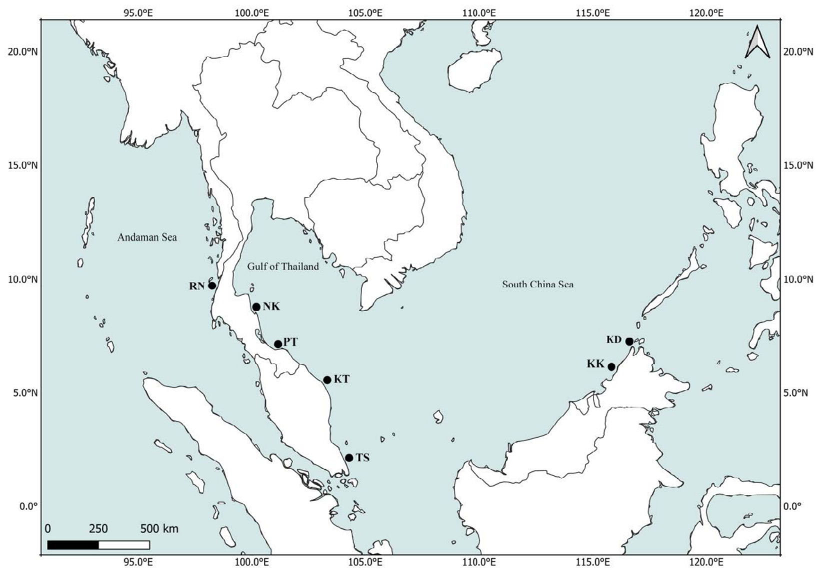

Figure 1. Map of sampling locations in Malaysia and southern Thailand.

Table 1. Definitions of morphometric characters of *Thenus* spp. Leach, 1816 used for this study based on Burton and Davie (2007).

No.	Measurement	Character Abbreviation	Definition
1	1 – 10	Tlength	Total length
2	1 – 16	CL	Carapace length
3	2 – 18	CW1	Carapace width 1
4	3 – 17	CW2	Carapace width 2
5	19 – 23	A1L	Antennae 1 length
6	20 – 22	A1W	Antennae 1 width
7	21 – 26	A2L	Antennae 2 length
8	24 – 25	A2W	Antennae 2 width
9	27 – 30	PL1	Propodus 1 length
10	35 – 38	PL2	Propodus 2 length
11	43 – 46	PL3	Propodus 3 length
12	28 – 29	PW1	Propodus 1 width
13	36 – 37	PW2	Propodus 2 width
14	44 – 45	PW3	Propodus 3 width
15	31 – 34	ML1	Merus 1 length
16	39 – 42	ML2	Merus 2 length
17	47 – 50	ML3	Merus 3 length
18	32 – 33	MW1	Merus 1 width
19	40 – 41	MW2	Merus 2 width
20	48 – 49	MW3	Merus 3 width
21	5 – 16	AL1	Abdomen segment 1 length
22	4 – 15	AW1	Abdomen segment 1 width
23	7 – 13	AL2	Abdomen segment 6 length
24	6 – 14	AW2	Abdomen segment 6 width
25	8 – 12	TL	Telson length
26	9 – 11	TW	Telson width

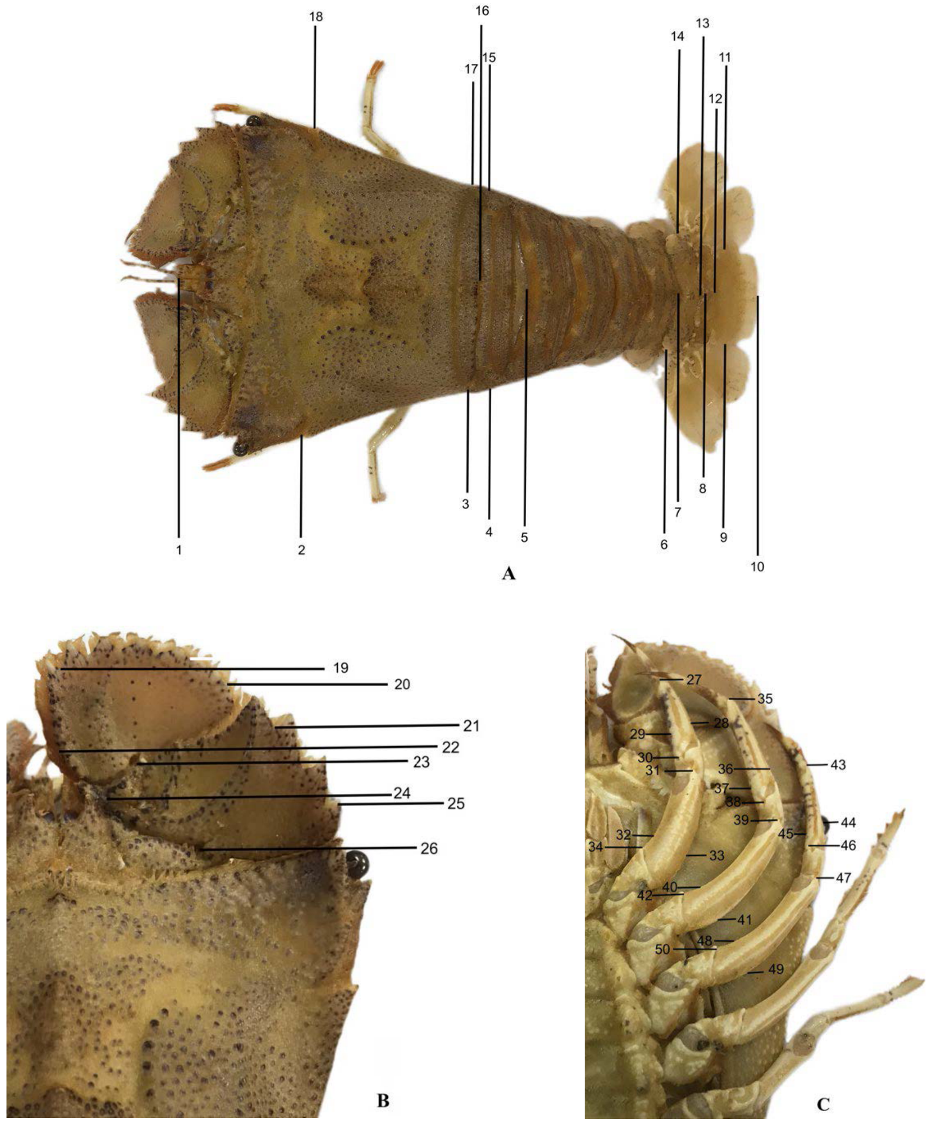

Figure 2. Morphometric measurements of *Thenus* spp. Leach, 1816. A: carapace and abdomen (dorsally measured); B: antennae; C: first, second, and third pereiopods. Modified from Burton and Davie (2007).

Data analysis

Descriptive statistics viz. mean, standard deviation, minimum value, and maximum value were produced for the morphometric measurements. The measurements were log-transformed for data linearization (Chandran et al., 2022). Size-dependent variation in the morphometric measurements was eliminated using the allometric method, proposed by Elliott et al. (1995). The equation was:

$$M_{adj} = M\left(\frac{L_s}{L_0}\right)^b$$

In the equation, M is the original measurement, M_{adj} is the adjusted measurement, L_0 is the total length of the slipper lobster, L_s is the overall mean of the total length for all the slipper lobsters from all sampling sites, and b is the slope of the regression of logM against $\log L_0$ using all slipper lobsters from all sampling sites. Successful removal of size variation was confirmed by testing the significance of the correlation between the adjusted measurements derived from the allometric method and the total length. Total length was excluded from subsequent multivariate analysis because it was used as a basis for the transformation (Jaferian et al., 2010; Siddik et al., 2016; Zhang et al., 2016).

Thus, the other twenty-five size-adjusted morphometric measurements of the carapace, antennae, abdomen, pereiopods, and telson of *Thenus* spp. (n = 107) were subjected to canonical discriminant function analysis (CDFA) and hierarchical cluster analysis (CA) to examine patterns of phenotypic variation (García-Dávila et al., 2005; Wardiatno et al., 2021). CDFA was conducted to detect significant morphometric character variation between sites. Factor loading values of more than 0.3 are deemed significant, of which 0.4 is more significant and 0.5 or higher is extremely significant (Nimalathasan, 2009). Therefore, only the loading values greater than 0.4 were considered significantly important. Cross-validated classification results from discriminant analysis were used to evaluate the accuracy of group classifications. Dendrograms derived from CA, based on squared Euclidean distances between the groups of centroids, were used to display the relation and degree of similarity between the analyzed groups. All the statistical analyses in this study were conducted using Microsoft Excel and SPSS v. 27.

RESULTS

General characteristics

Table 2 shows the number of specimens collected by sex, and the range and mean (± SD) values for the total length (cm) and total weight (g) of *Thenus* spp. from the seven sampling locations in Malaysia and southern Thailand. Supplementary Material 1 shows the mean (± SD) lengths of the twenty-five morphometric characters of *Thenus* spp. analyzed by sites. Individuals of *T. orientalis* were collected from four sites (Kota Kinabalu; Kudat; Pattani; and Nakhon Si Thammarat), while *T. indicus* specimens were collected from six sites (Kota Kinabalu; Kuala Terengganu; Tanjung Sedili; Pattani; Nakhon Si Thammarat; and Ranong). The total length and weight of overall individuals collected ranged from 11.9 to 24.4 cm and 56.0 to 291.0 g for *T. orientalis*; and 10.8 to 26.7 cm and 35.0 to 312 g for *T. indicus*, respectively. The largest *T. orientalis* specimen was collected from the Kudat site (female, 24.4 cm, 291.0 g) while the smallest specimens were collected from the Pattani site (male, 11.9 cm, 60.7 g; and male, 12.84 cm, 56.0 g). Specimens of *T. orientalis* that were collected from the Nakhon Si Thammarat site had the highest mean values of total length and weight (19.5±2.56 cm, 195.5±47.19 g) while the smallest values were from Pattani (14.6±2.88 cm, 99.6±45.86 g). *T. indicus* specimens collected from the Ranong site had the highest mean total length and weight (18.6±1.50 cm, 177.2±12.2 g) while specimens from the Tanjung Sedili site had the lowest (13.1±0.95cm, 67.3±11.53 g). The largest *T. indicus* specimen was collected from the Kota Kinabalu site (female, 26.7 cm, 312.0 g), while the smallest specimens were collected from the Pattani (male, 10.8 cm, 52.9 g) and Kuala Terengganu (female, 11.0 cm, 35.0 g) sites. These three individuals also comprise the largest and smallest *Thenus* specimens collected in the whole study. In terms of sex, females were generally larger than males for all both species, of which the largest specimen collected overall was the female *T. indicus* from Kota Kinabalu.

Table 2. Total length (mean±SD, cm) and weight (mean±SD, g) of *Thenus* spp. Leach, 1816 specimens analyzed in this study from Malaysia and southern Thailand.

Location	Species	Num. of specimens		Total length (cm)		Total weight (g)	
		Male	Female	Range	Mean±SD	Range	Mean±SD
Kota Kinabalu	*T. orientalis*	15	7	12.4 – 24.0	15.9 ± 3.51	67.1 – 247.0	120.3 ± 61.48
	T. indicus	2	6	13.1 – 26.7	15.9 ± 4.51	63.6 – 312.0	111.0 ± 81.97
Kudat	*T. orientalis*	1	6	15.8 – 24.4	17.9 ± 3.00	92.0 – 291.0	160.1 ± 62.96
Kuala Terengganu	*T. indicus*	5	5	11.0 – 22.2	14.6 ± 4.27	35.0 – 154.0	74.6 ± 43.34
Tanjung Sedili	*T. indicus*	7	2	11.5 – 14.5	13.1 ± 0.95	55.0 – 83.0	67.3 ± 11.53
Pattani	*T. orientalis*	8	5	11.9 – 20.7	14.6 ± 2.88	56.0 – 216.0	99.6 ± 45.86
	T. indicus	8	7	10.8 – 17.0	14.1 ± 1.84	52.9 – 158.4	94.0 ± 32.59
Nakhon Si Thammarat	*T. orientalis*	5	4	16.4 – 24.2	19.5 ± 2.56	129.0 – 280.7	195.5 ± 47.19
	T. indicus	2	9	15.1 – 20.5	17.1 ± 1.55	108.6 – 206.4	146.5 ± 28.17
Ranong	*T. indicus*	3	3	16.6 – 20.6	18.6 ± 1.50	160.2 – 193.2	177.2 ± 12.21

Phenotypic variation between sites

Between the four sites where *T. orientalis* were collected, the CDFA provided three canonical discriminant functions with Wilk's lambda values ranging from 0.0001 to 0.26, with statistically significant values ($p < 0.01$) (Table 3). The first function provided 77.2% of the total variance between sites, while the second function contributed 18.0%, so the first two factors cumulatively explained 95.2% of the entire variation. The third function had weak discriminatory power and only explained 4.8% of the total variance. In the first function, the morphometric characters with the greatest effect in separating the sites of *T. orientalis* were CW2, A1L, A2L, ML1, MW2, ML3, MW3, AL1, and AW1 (Table 4). Overall, the variation between *T. orientalis* sites was best explained by the width of the merus of the third pereiopods (MW3), the width of the sixth abdomen segment (AW2), and the width of the posterior margin of the carapace (CW2) by DF1, DF2, and DF3, respectively. By comparison, these characters were notably greater in size in the Nakhon Si Thammarat specimens than the Pattani, Kota Kinabalu, and Kudat specimens (Supplementary Material 1).

Table 3. Summary of canonical discriminant function and Wilk's lambda test for verifying differences between the sites for *T. orientalis* and *T. indicus,* respectively, morphometric characters using CDFA.

Species	Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Wilks' Lambda	Chi-square	df	Sig.
	1	42.73	77.2	77.2	0.99	0.0001	250.3	75	0.0001
T. orientalis	2	10.92	18.0	95.2	0.96	0.02	124.68	48	0.0001
	3	2.89	4.8	100.0	0.86	0.26	44.14	23	0.005
	1	223.33	85.1	85.1	0.99	0.0001	526.4	125	0.0001
	2	31.50	12.0	97.1	0.98	0.001	296.34	96	0.0001
T. indicus	3	4.30	1.6	98.8	0.90	0.03	148.39	69	0.0001
	4	2.34	0.9	99.7	0.837	0.16	77.51	44	0.001
	5	0.85	0.3	100.0	0.679	0.54	26.23	21	0.198

Table 4. The standardized canonical discriminant function coefficients from CDFA of *T. orientalis* and *T. indicus* between sites, respectively.

Character	Species						
	T. orientalis			*T. indicus*			
	DF1	DF2	DF3	DF1	DF2	DF3	DF4
CL	-	-	-	-	1.69	-	-
CW1	-	-	0.63	-	-	0.64	-
CW2	1.52	0.99	2.54	0.38	-	0.55	1.21
A1L	0.39	1.48	0.63	-	-	-	0.56
A1W	-	1.4	-	-	-	0.59	-
A2L	1.23	-	1.01	-	-	0.7	-
A2W	-	-	-	2.51	-	-	-
PL1	-	-	-	-	-	-	0.42
PW1	-	-	0.69	0.67	-	-	-
ML1	2.18	-	0.36	1.14	1.43	-	0.35
MW1	-	-	-	-	3.02	-	1.34
PL2	-	-	0.21	0.38	-	-	-
PW2	-	-	-	-	-	-	-
ML2	-	1.09	0.33	-	0.69	-	-
MW2	1.04	0.72	2.28	-	-	-	-
PL3	-	-	-	-	-	0.52	0.57
PW3	-	-	-	-	-	-	-
ML3	0.33	1.68	-	0.93	0.97	0.63	-
MW3	2.23	0.79	0.7	-	-	-	-
AL1	0.65	0.5	0.34	-	-	-	-
AW1	1.92	0.88	-	-	2.24	-	1.24
AL2	-	-	0.49	0.78	-	1.00	-
AW2	-	2.75	-	-	-	-	-
TL	-	-	1.43	0.91	-	0.81	0.62
TW	-	0.66	-	0.79	1.47	-	-

Note: DF = discriminant function

The scatter plot revealed significant differences between the four sites as distinct centroids (Figure 3a). While the *T. orientalis* cases of Kota Kinabalu and Kudat showed a high degree of overlap to form one group, the cases of Pattani and Nakhon Si Thammarat formed two separate groups. Cross-validation classification showed that the discriminant analysis correctly classified 85.4% of the *T. orientalis* specimens from the four sites overall (Table 5). The best cross-validated classification rate was obtained for Nakhon Si Thammarat cases at 100%, followed by Kudat cases at 85.7%. Also, the cross-validation classification results showed two intermixing groups occurring as (i) Pattani and Kota Kinabalu and (ii) Kota Kinabalu and Kudat. Meanwhile, the Nakhon Si Thammarat cases stood alone. The dendrogram shows the relation of the *T. orientalis* sites as two main clusters, where the cases of Kota Kinabalu and Kudat formed one cluster, while the cases of Pattani and Nakhon Si Thammarat formed the other cluster before fragmenting into individual groups (Figure 4a).

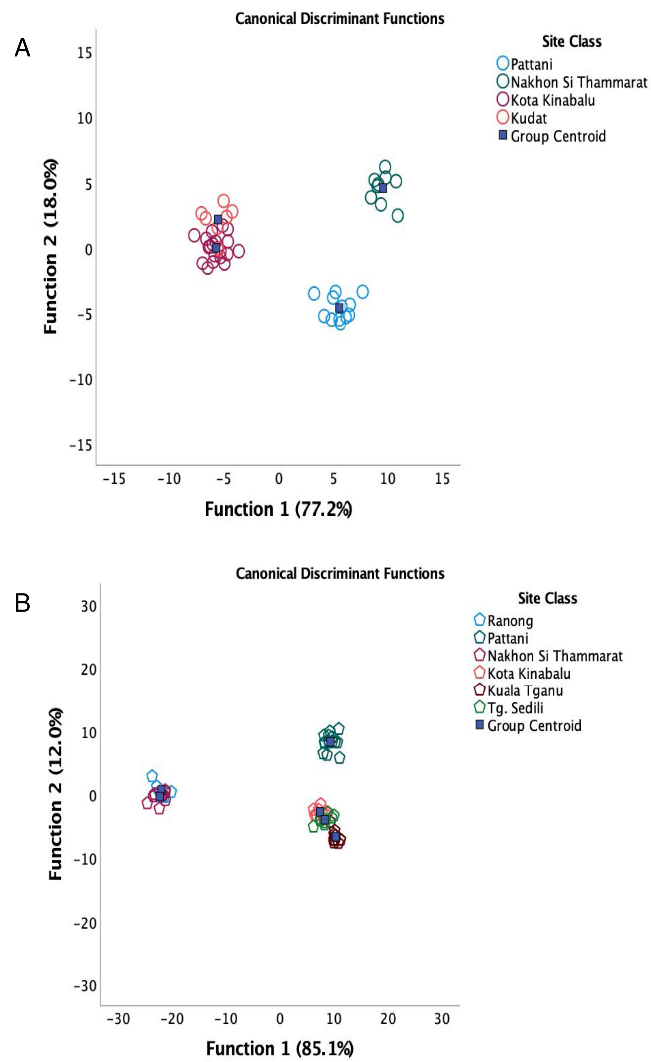

Figure 3. Scatterplot of the discriminant function scores from the analysis of 25 morphometric characters for *Thenus* spp. from Malaysia and Thailand. A, four sites of *T. orientalis* Lund, 1793 (n = 48); and B, six sites of *T. indicus* Leach, 1816 (n = 59).

A

B

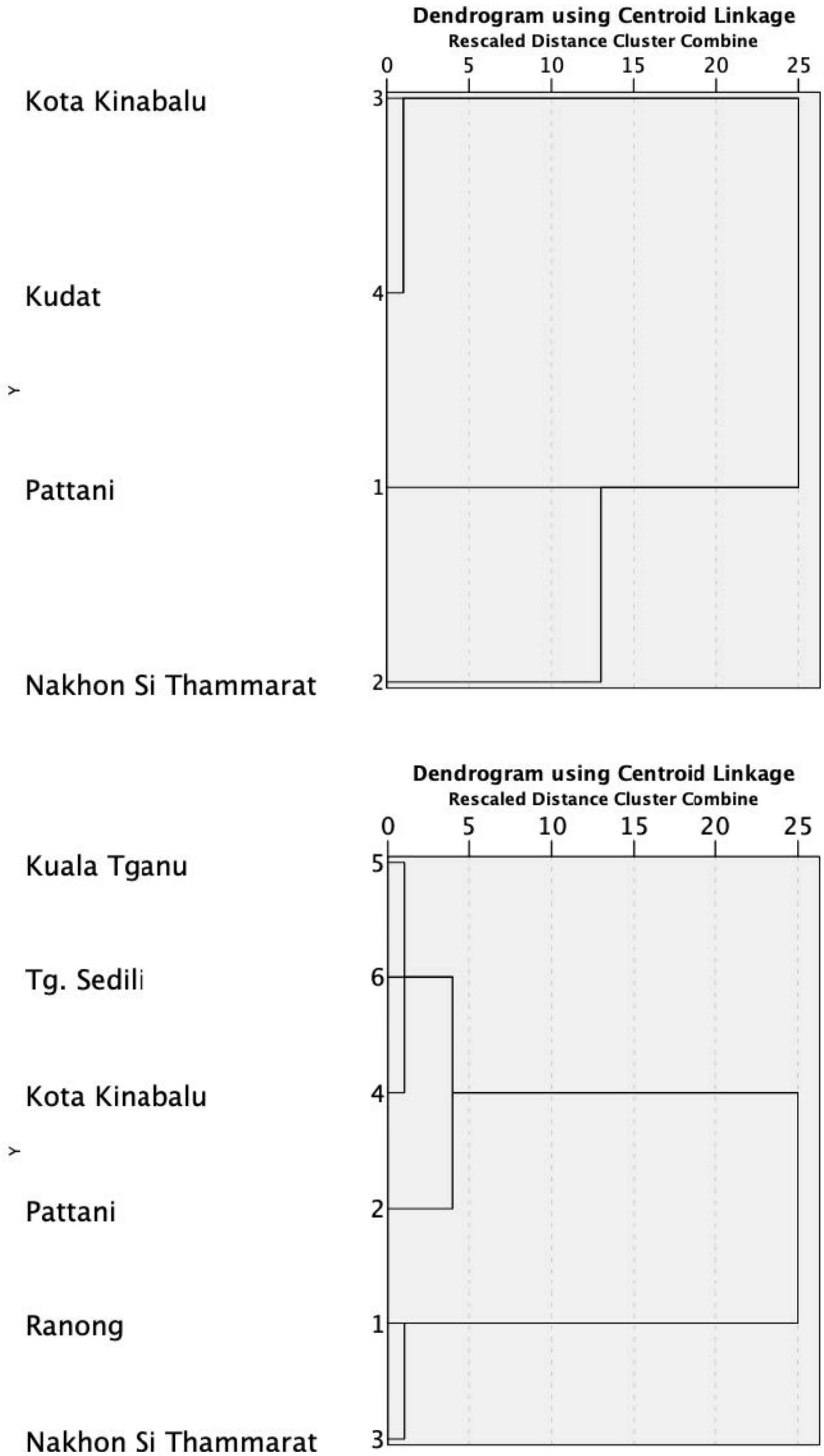

Figure 4. Dendrogram derived from cluster analysis of morphometric characters based on squared Euclidean distances between the groups of centroids. A, four sites of *T. orientalis* Lund, 1793; and B, six sites of *T. indicus* Leach, 1816 from Malaysia and Thailand. The horizontal axis numbers indicate average joins among populations.

Table 5. Predicted classification results from discriminant analysis among sites for *T. orientalis* and *T. indicus*, respectively. Numbers in bold indicate the percentage of classification success (%). Corresponding numbers of individuals are shown in parentheses.

Site	Original group membership (100.0%)						Cross-validated group membership (85.4%)						
T. orientalis	PT		NK	KK	KD		PT	NK	KK		KD		Total
PT	100 (12)		0.0 (0)	0.0 (0)	0.0 (0)		83.3 (10)	8.3 (1)	8.3 (1)		0.0 (0)		100 (12)
NK	0.0 (0)		100 (9)	0.0 (0)	0.0 (0)		0.0 (0)	100 (9)	0.0 (0)		0.0 (0)		100 (9)
KK	0.0 (0)		0.0 (0)	100 (2)	0.0 (0)		5.0 (1)	0.0 (0)	80.0 (16)		15.0 (3)		100 (20)
KD	0.0 (0)		0.0 (0)	0.0 (0)	100 (7)		0.0 (0)	0.0 (0)	14.3 (1)		85.7 (6)		100 (7)
T. indicus	Original group membership (100.0%)						Cross-validated group membership (86.4%)						
	RN	PT	NK	KK	KT	TS	RN	PT	NK	KK	KT	TS	Total
RN	100 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	83.3 (5)	0.0 (0)	16.7 (1)	0.0 (0)	0.0 (0)	0.0 (0)	100 (6)
PT	0.0 (0)	100 (15)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (15)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (15)
NK	0.0 (0)	0.0 (0)	100 (11)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (11)	0.0 (0)	0.0 (0)	0.0 (0)	100 (11)
KK	0.0 (0)	0.0 (0)	0.0 (0)	100 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	75.0 (6)	12.5 (1)	12.5 (1)	100 (8)
KT	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (10)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	20.0 (2)	50.0 (5)	30.0 (3)	100 (10)
TS	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (9)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100 (9)	100 (9)

Note: PT = Pattani, NK = Nakhon Si Thammarat, KK = Kota Kinabalu, KD = Kudat, RN = Ranong, KT = Kuala Terengganu, TS = Tanjung Sedili.

Between the six sites where *T. indicus* were collected, the CDFA yielded four canonical discriminant functions with Wilk's lambda values ranging from 0.0001 to 0.16 and significant chi-square values ($p < 0.001$). The first two functions cumulatively explained 97.1% of the total variation, for which the first function contributed the most to the total variance between sites at 85.1%, followed by the second function at 12.0% (Table 3). The third and fourth functions contributed very little to the total variance – 1.6% and 0.9%, respectively – and had extremely poor discriminatory power. The fifth function was not statistically significant. The morphometric characters with the greatest impact on separating sites of *T. indicus* in the first function were A2W, PW1, ML1, ML3, AL2, TL, TW, and CW2 (Table 4). A2W explained most of the variation in the first function, while AL2 explained most of the variation in the third function, and MW1 explained most of the variation in the second and fourth functions. Overall, the morphometric characters that best discriminated *T. indicus* sites were the width of the second antenna (A2W), the length of the sixth abdomen segment (AL2), and the width of the merus of the first pereiopods (MW1). Generally, specimens from Pattani, Tanjung Sedili, and Kuala Terengganu had smaller widths in their second antennae and merus of the first pereiopods compared to those of the other three sites (Supplementary Material 1). They also had greater lengths in their sixth abdomen segments compared to those of the other sites except for Kota Kinabalu.

The scatter plot displays a high degree of overlap in the morphometric data between the sites with distinct but close centroids forming three groups: (i) Ranong and Nakhon Si Thammarat; (ii) Kota Kinabalu, Tanjung Sedili, and Kuala Terengganu, and (iii) Pattani (Figure 3b). The overall cross-validated classification results show that 86.4% of the *T. indicus* specimens were correctly classified for the six sites (Table 6). The best cross-validated classification rates were obtained for the *T. indicus* cases in Pattani, Nakhon Si Thammarat, and Tanjung Sedili, each at 100% with no intermixing observed with other sites. The cross-validated classification results indicated two intermixing groups: (i) Ranong and Nakhon Si Thammarat, (ii) Kota Kinabalu, Kuala Terengganu, and Tanjung Sedili. The dendrogram provided clarity on the relation by showing the degree of similarity between the overlapping cases (Figure 4b). The sites are initially divided into two clusters: Nakhon Si Thammarat and Ranong cases in one cluster, and the Pattani and Malaysian cases in the other. The cases of Kuala Terengganu, Tanjung Sedili, and Kota Kinabalu are clustered further, apart from the Pattani cases, to form a sub-cluster.

DISCUSSION

Thenus was previously considered monotypic, with *T. orientalis* Lund, 1793 as the sole member. However, Burton and Davie (2007) published a taxonomic review distinguishing five separate *Thenus* species based on morphological characteristics, morphometric ratios, and molecular data. Since then, *Thenus* populations have been studied worldwide to corroborate species composition and distribution, such as in India (Jeena et al., 2015; Anuraj et al., 2017) and Indonesia (Wardiatno et al., 2016; Wiadnyana et al., 2019). This study updates distribution records of *Thenus* spp. in Malaysia and southern Thailand, where a total of two species of *Thenus* were found. *T. indicus* was the most frequently captured species in the trawl fisheries of both countries, as it was collected in most of the landing sites. The *T. indicus* collection in Ranong updated a past distribution report on *Thenus* spp. in Thailand that expected this species to be present, but did not report it (Iamsuwansuk et al., 2012). Contrastingly, *T. orientalis* was not found in the Andaman Sea, but was prevalent in the sites of the Gulf of Thailand and the South China Sea. This study collected *T. indicus* specimens from Tanjung Sedili, which is also an update on the distribution range of this species, since past reports had only noted *T. orientalis* in Johor waters (Siow et al., 2018, 2020). Iamsuwansuk et al. (2012) suggested that the distribution pattern of *Thenus* spp. in the region is influenced by the availability of preferred habitat conditions of each species, in which *T. indicus* prefer shallower water close to the coast, while *T. orientalis* were more common in the deeper waters of the open sea (Iamsuwansuk et al., 2012). For sediment composition, *T. orientalis* tend to inhabit sandy, coarse, and muddy substrates with shells and gravel (Kizkhakudan et al., 2004; Chan et al., 2011; Saher et al., 2018), while *T. indicus* prefer fine mud and silty inshore substrates (Butler et al., 2011). The pereiopods are particularly significant in scyllarid feeding and concealment behavior (Lau, 1987; Jones, 2007). *Thenus* spp. are highly skilled in handling and opening shells using their pereiopods (Lau, 1987), which supports their preference for molluscan prey (Jones, 2007). The pereiopods, as well as the abdomen and antennal segments, are also involved in the hydrodynamics of scyllarid swimming (Spanier et al., 2010).

Multivariate analyses on twenty-five morphometric characters were successful in demonstrating significant phenotypic variation between selected sites for *T. orientalis* and *T. indicus*. The results of the CDFA and CA supported each other in displaying the patterns of significant phenotypic variation between selected sites for *T. orientalis* and *T. indicus*. Between the four sites for *T. orientalis*, the morphometric data showed significant phenotypic variation and separated the sites into three groups viz. (i) Kota Kinabalu and Kudat, (ii) Pattani, and (iii) Nakhon Si Thammarat. The strongest predictors were the pereiopods, abdomen, and carapace. These elements were larger in the Nakhon specimens than in those of Pattani, Kota Kinabalu, and Kudat. Kota Kinabalu and Kudat share similar morphometric data, suggesting a subpopulation of *T. orientalis* in Sabahan waters, while Pattani and Nakhon form separate clusters, suggesting two distinct subpopulations of *T. orientalis* occurring in the lower Gulf of Thailand. Intermixing morphometric data between specimens of Pattani and Kota Kinabalu suggests morphological similarities between the individuals of these two distant sites. Between the six sites for *T. indicus*, the morphometric data showed significant phenotypic variation and separated the sites into three groups viz. (i) Ranong and Nakhon Si Thammarat; (ii) Kota Kinabalu, Tanjung Sedili, and Kuala Terengganu; and (iii) Pattani. The best descriptors were the antenna, pereiopods, and abdomen, and the specimens of Pattani, Tanjung Sedili, and Kuala Terengganu, differed from the other three sites in these characters. The three Malaysian sites showing very similar morphometric data suggest a single population of *T. indicus* occurring in Malaysian waters. The CA dendrogram showing the Pattani specimens clustering with the Malaysian sites rather than Nakhon, suggests a close morphological similarity between contiguous sites that does not extend further up the Gulf. This suggests that two distinct subpopulations might exist in the lower Gulf for *T. indicus*, as well. The morphological characters that best differentiated individuals were those related to feeding, burying, and swimming, namely the pereiopods, abdomen, and antenna. This may suggest that the variations observed might be due to adaptations to the local habitat and environmental conditions (Zhang et al., 2016; Chandran et al., 2022). The Gulf's bathymetry (Morley, 2015; Waewsak et al., 2015) and seasonal current circulations (Sojisuporn et al., 2010; Wang et al., 2020) may play a role in affecting movement and food availability. Ranong and Nakhon specimens clustering together suggests they share morphological similarities despite being the most geographically distant, occurring in two separate waterbodies on either side of Thailand. This may indicate that the two locations share similar environmental conditions (Zhang et al. 2016; Wardiatno et al., 2021). Further study is required to confirm the similarities and differences in habitat and environmental conditions between these locations.

This study characterized the populations of *Thenus* spp. in Malaysia and Thailand, which can serve as baseline information for sustainable fisheries management, especially in spatial planning. Morphometric differences suggest a complexity of stock structure, possibly indicating subpopulations that would require fisheries managers to redefine management units for the best strategy of exploitation (Zhang et al., 2016; Wardiatno et al., 2021). Common spatial tools in fisheries management within the region are fishing zones and marine protected areas (Garces et al., 2006; Nootmorn, 2020). If existing management zones are inconsistent with assemblage patterns, fishermen are potentially fishing the same stock despite sectors being spatially segregated (Garces et al., 2006). Although fishing zones in the Malaysian exclusive economic zone (EEZ) are segregated state-wise, the fishermen may be fishing the same stock of *Thenus* spp. It would be valuable for monitoring purposes to know that similar habitat conditions in distant sites develop similar morphometric data. A population study for *T. indicus* in the upper Gulf of Thailand found it to be genetically homogenous (Iamsuwansuk et al., 2012), while this study found *T. indicus* in the lower Gulf to be phenotypically varied, which suggests a possible divide between Nakhon and Pattani that should be considered for fisheries management. It is important to note isolated spatial structures during management to maintain spawning components and genetic diversity (Zhang et al., 2016). Regional efforts with neighboring countries collaboration to manage *Thenus* spp. may be possible due to the morphometric similarity between Pattani and Malaysian sites, indicating phenotypic homogeneity between contiguous sites.

Further studies should explore the genetic characteristics between sites to clarify the morphological homogeneity, especially between geographically distant sites. An analysis of the genetic diversity of *Thenus* spp. in Malaysian waters might also observe a narrow genetic diversity between sites to support the homogeneous phenotypic data. A genetic study in the lower Gulf of Thailand would also be informative to investigate a possible genetic barrier between the two sites.

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AUTHOR CONTRIBUTIONS

I.H.R.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

C.C.A.: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

S.H.: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

K.K.S.: Formal analysis, Methodology, Validation, Visualization, Writing – review & editing.

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