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DNA Barcoding of Commercially Important Trevallies, *Carangoides* spp. (Carangiformes: Carangidae): A Baseline Report of Species from Malaysia

Nuralif Fakhrullah Mohd Nur[1] · Salwani Abdullah[1] · Ying Giat Seah[1] · Siti Azizah Mohd Nor[2] · Min Pau Tan[2] · Ahasan Habib[1] · Rumeaida Mat Piah[1] · Tun Nurul Aimi Mat Jaafar[1]

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Abstract
Species of genus *Carangoides* also known as trevallies are one of the commercially exploited groups of fishes in Malaysia. The genus *Carangoides* consists of fishes with mixed morphological and meristic characteristics. Due to this, species within this genus are often reported as single collective group, rather than as an individual species. Thus, fisheries landing statistics do not reflect the precise number of individual species harvested and the true status of species exploitation pattern will hinder efficient sustainable exploitation of a particular species. In this study, an annotated list of the 13 species of *Carangoides* known from Malaysian waters is presented with two species (*C. oblongus* and *C. talamparoides*) recorded as first specimen-based records and two species (*C. chrysophrys* and *C. fulvoguttatus*) as additional specimen-based distribution records in Malaysia. All species are briefly described, and a key is provided to identify Malaysian species of *Carangoides*. The mitochondrial Cytochrome c oxidase subunit I (COI) gene was also analyzed for genetic identification of 271 samples representing all of the species in the study. The average within species K2P distance was 0.4% with *C. oblongus* and *C. praeustus* showing the lowest intraspecific divergence (0%) and *C. coeruleopinnatus* showed the highest (1.3%). A maximum-likelihood tree generated from haplotype sequences clearly grouped all 13 putative species into their own clade. However, *C. coeruleopinnatus* and *C. gymnostethus* showed deep intraspecific divergence (9.1% and 3.5%) which formed three and two clusters with their own respective taxa. A more detailed analysis on the taxonomic status of some individuals within these species is required.

Keywords *Carangoides* · DNA-based taxonomy · Fish diversity · Indo-Malay · Molecular identification

Introduction

The genus *Carangoides* is one of the important components in the marine ecosystem, with several species supporting large commercial and recreational fisheries throughout the world's oceans (FAO 2018). As such, *Carangoides* also one of the major commercial fish groups in the biodiverse Indo-Malay Archipelago (IMA) region, which includes Malaysia (DOF 2019). The genus *Carangoides* is a member of the family Carangidae (Carangiformes), which consists of 18 valid species worldwide (Fricke et al. 2015). Species in this genus vary in size and shape and often appear morphologically similar to confamilial members such as other jacks (*Caranx*) and trevallies (*Atropus* and *Ulua*). Most of the species are widely distributed in the subtropical and tropical marine environment of the Indo-Pacific and Atlantic Oceans (Gaither et al. 2016). Residing within the Indo-Pacific Ocean, the South China Sea, Straits of Malacca, the Sulu Sea, and the Celebes Sea offer immense opportunities for exploitation of various commercially important fish species in this biodiverse region including the *Carangoides*. According to FishBase (Froese and Pauly 2019), Malaysia lies within this unique biogeographic region and supports 16 of the 18 global species of *Carangoides* in her surrounding waters. Exploited by various fishing gears throughout the year, *Carangoides* catches are usually mixed with

✉ Tun Nurul Aimi Mat Jaafar
tun_aimi@umt.edu.my

[1] Faculty of Fisheries and Food Science, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia

[2] Institute of Marine Biotechnology, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia

representation of three or more species in local markets. *Carangoides* is rarely reported as separate species due to almost similar morphology among several members of the genus and therefore pose a great challenge in documenting the precise number of species available in Malaysia.

The taxonomy of *Carangoides* is poorly understood and their generic limits were not well defined (Gunn 1990; Reed et al. 2002). *Carangoides* was first recognized by Pieter Bleeker in 1851. Later, much of the early works on Indo-West Pacific carangids were carried out by Forsskål (1775), Rüppell (1828–1830) and Bleeker (1852). The genus *Carangoides* has been described and reviewed by various fish taxonomists in their respective countries with a number of new species been recorded (Gunn 1990; Kim et al. 1999, 2008; Lin and Shao 1999; Lim et al. 2010; Bogorodsky et al. 2017), however, no study was reported from Malaysia. Classification of *Carangoides* was very challenging due to morphological and meristic similarities across species, as well as plasticity in body shape, size and color patterns (Froese and Pauly 2019). In addition, *Carangoides* typically display significant changes in morphology and pigmentation during growth, and such changes have likely led to misidentification of specimens and contributed to general taxonomic confusion. This has resulted many species being described, yet many of which were synonyms (Joshi et al. 2011; Smith-Vaniz and Carpenter 2015).

Traditionally, species identification had been based on morphological differentiation, but it is now widely acknowledged that molecular data is also necessary for taxonomic revisions (Darlina et al. 2011; Habib and Sulaiman 2016; Aaron et al. 2018; Du et al. 2019). Sequencing of mitochondrial DNA (mtDNA) Cytochrome oxidase subunit I (COI) gene or, popularly known as the DNA barcode marker for animals is an established approach with an international campaign, FISH-BOL (www.fishbol.org) aimed to barcode all fish in the world. The COI gene has successfully discriminated a wide range of fishes from marine (Bakar et al. 2018; Chu et al. 2019; Rabaoui et al. 2019; Thu et al. 2019; Fadli et al. 2020) to freshwater environments (Muchlisin et al. 2013; Barman et al. 2018; Rahman et al. 2019; Tan et al. 2019). However, the success of species identification through DNA barcoding approach depends on the accuracy of species identification in DNA barcode library, namely GenBank and BOLD System (Seah et al. 2017). Misidentification of species in the barcode library will lead to misinterpretations of global biodiversity.

DNA barcoding is not only useful for species identification and delimitation, but also permits the discovery of new species and identification of cryptic diversity (Bakar et al. 2018; Lim et al. 2016; Martinez-Takeshita et al. 2015; Mat Jaafar et al. 2020a). Cryptic species are two or more species that are morphologically similar yet genetically distinct. Because of their morphological similarities, cryptic species are identified as the same species in the existing system. Using the DNA barcoding approach, any atypically large genetic distance between pairwise comparisons of members of a particular species could be flagged as a potential cryptic species. It is not unexpected that the biodiversity hotspot within the IMA and its component seas support a myriad of cryptic diversity (Mat Jaafar et al. 2012). For example, a study on the Carangidae biodiversity within the IMA revealed that although all morphologically described species formed monophyletic clusters, there were several instances of likely occurrence of cryptic diversity within potential species complex, however, none involving species of *Carangoides* (Mat Jaafar et al. 2012). From the same study, an initial reference library for this family was generated, including the barcode of eight presumed species of *Carangoides*, however, it was still incomplete (Mat Jaafar et al. 2012). In addition, little research was conducted to assess the taxonomic ambiguities in *Carangoides.* Therefore, the current study was initiated to record all *Carangoides* species available in Malaysian waters, that comprise of the South China Sea, Straits of Malacca, the Sulu Sea, and the Celebes Sea, as well as to expand a reliable DNA barcode library of *Carangoides* fishes within the IMA. Here, the first formal description of 13 species of *Carangoides* from Malaysia was provided, including the diagnostic keys, photographs, and selected characters for species identification. Nevertheless, correct identification of this genus at all life stages is of critical importance for an effective fisheries management, trading, and conservation purposes.

Materials and Methods

Sample Collections

A total of 589 specimens of *Carangoides* (Table 1) were collected along the coast of Malaysia (Fig. 1). All specimens were morphologically identified into 13 species using taxonomic keys and fish identification references from Lin and Shao (1999); Smith-Vaniz (1999); Ambak et al. (2010); Yoshida et al. (2013) and Ahmad et al. (2018). For DNA analyses, a total of 144 fin clips were removed from the right pectoral fin of each fish and preserved in 99% ethanol. Fish specimens were then placed in ice, frozen on site and transported to Fisheries Science Laboratory, Faculty of Fisheries and Food Science, Universiti Malaysia Terengganu (UMT), Malaysia. Voucher specimens were deposited at the South China Sea Repository and Reference Centre (RRC), Institute of Oceanography and Environment (INOS), UMT with voucher numbers UMTF9385 – UMTF9534.

Morphometric Measurements and Meristic Counts

Guideline for measurement was illustrated in Fig. 2. Meristic and morphometric methods generally followed the standard

Table 1 Species of *Carangoides* collected and sample sizes analysed for mtDNA COI

Species	South China Sea						Straits of Malacca			Sulu Sea			Celebes Sea			Total sample sizes analysed for COI in current study
	Peninsular Malaysia			East Malaysia												
	Mat Jaafar et al. (2012)	BOLD (2012)	**Current Study**	Mat Jaafar et al. (2012)	BOLD (2012)	**Current Study**	Mat Jaafar et al. (2012)	BOLD (2012)	**Current Study**	Mat Jaafar et al. (2012)	BOLD (2012)	**Current Study**	Mat Jaafar et al. (2012)	BOLD (2012)	**Current Study**	
C. armatus	-	5	6 (18)	-	2	2 (2)	-	-	4 (12)	-	-	1 (2)	-	-	-	13
C. bajad	-	1	2 (3)	-	-	-	-	-	-	-	-	-	-	-	1 (2)	3
C. chrysophrys	-	-	17 (34)#	9	-	2 (10)	1	-	-	8	-	-	1	-	-	19
C. coeruleopinnatus	13*	-	18 (78)#	9*	-	3 (14)	1*	(1)	11 (18)	8*	(2)	2 (10)	1*	-	1 (2)	35
C. dinema	-	-	-	-	-	1 (6)	-	-	-	1	-	2 (14)	5	-	2 (9)	5
C. ferdau	-	-	-	-	-	1 (1)	2	-	3 (4)	-	-	-	-	-	-	4
C. fulvoguttatus	3	-	5 (19)	-	-	-	-	-	1#	-	-	(5)#	-	-	1 (1)#	7
C. gymnostethus	9**	-	4 (18)	11**	-	4 (9)	1	-	1 (1)	6**	-	1 (4)	-	-	1 (1)	11
C. hedlandensis	3	(5)	8 (33)	-	-	5 (22)	-	3	1 (4)	-	3	1 (4)	-	4	1 (2)	16
C. malabaricus	-	-	4	-	-	6 (21)	-	-	5 (27)	-	-	1	-	-	1	17
C. oblongus^	-	-	-	-	-	1 (1)	-	-	1 (1)	-	-	2 (6)	-	1	-	4
C. praeustus	-	-	-	-	-	-	-	-	-	-	-	1 (1)	-	-	2 (10)	3
C. talamparoides^	-	-	-	-	-	1 (6)	-	-	2 (6)	-	-	3 (3)	-	-	1 (1)	7
TOTAL																**144**

*In Mat Jaafar et al. (2012) identified as *C. malabaricus*, **In Mat Jaafar et al. (2012) identified as *C. bajad*, #Additional specimen-based distribution records, ^ First specimen-based records, () Actual samples collected to show biodiversity abundance

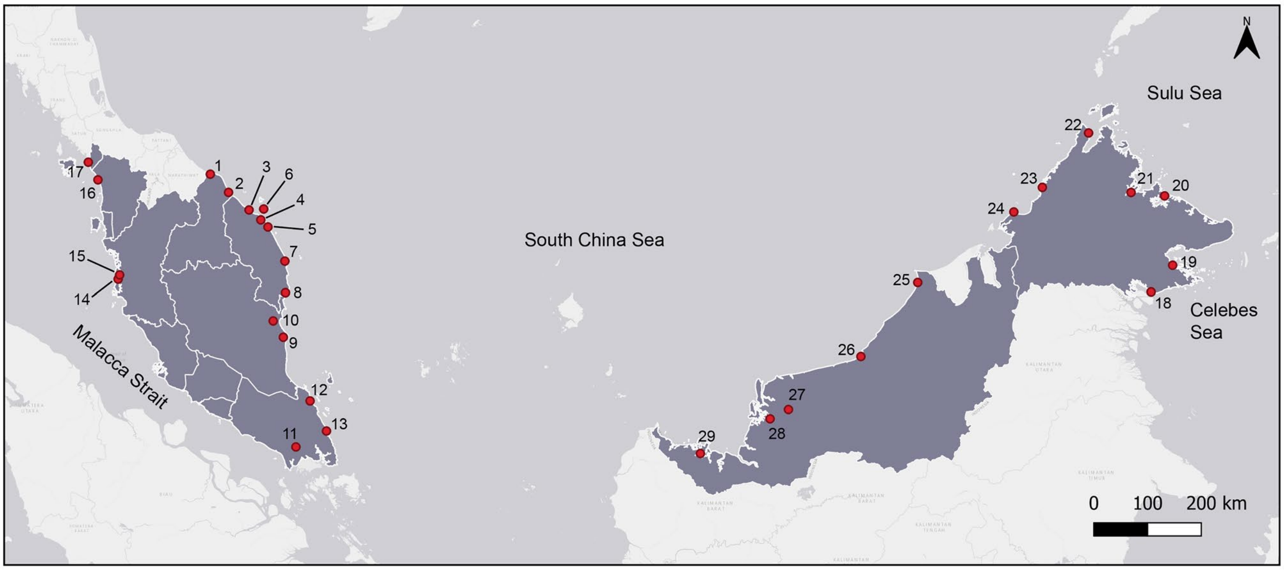

Fig. 1 Sampling area of *Carangoides* spp. along coast of Malaysia. East Coast of Peninsular Malaysia (1: Tumpat; 2: Tok Bali; 3: Penarik; 4: Batu Rakit; 5: Pulau Kambing; 6: Pulau Bidong; 7: Kuala Dungun; 8: Chukai Kemaman; 9: Pekan; 10: Kuantan; 11: Kulai; 12: Mersing; 13: Tanjung Sedili); West Coast of Peninsular Malaysia (14: Pantai Remis; 15: Bagan Panchor; 16: Kuala Kedah; 17: Kuala Perlis) and East Malaysia (18: Tawau; 19: Kunak; 20: Sandakan; 21: Beluran; 22: Kudat; 23: Kota Kinabalu; 24: Kuala Penyu; 25: Miri; 26: Bintulu; 27: Sibu; 28: Sarikei; 29: Kuching)

procedures outlined by Hubbs and Lagler (1964) and Gushiken (1983). Morphospecies identification were based on Matsunuma et al. (2011); Ambak et al. (2010), Fricke et al. (2015); Smith-Vaniz (1999); Mansor et al. (1998); Mohsin and Ambak (1996) and FAO–Fisheries Identification Sheets (Fischer and Whitehead 1974). Samples from different size and

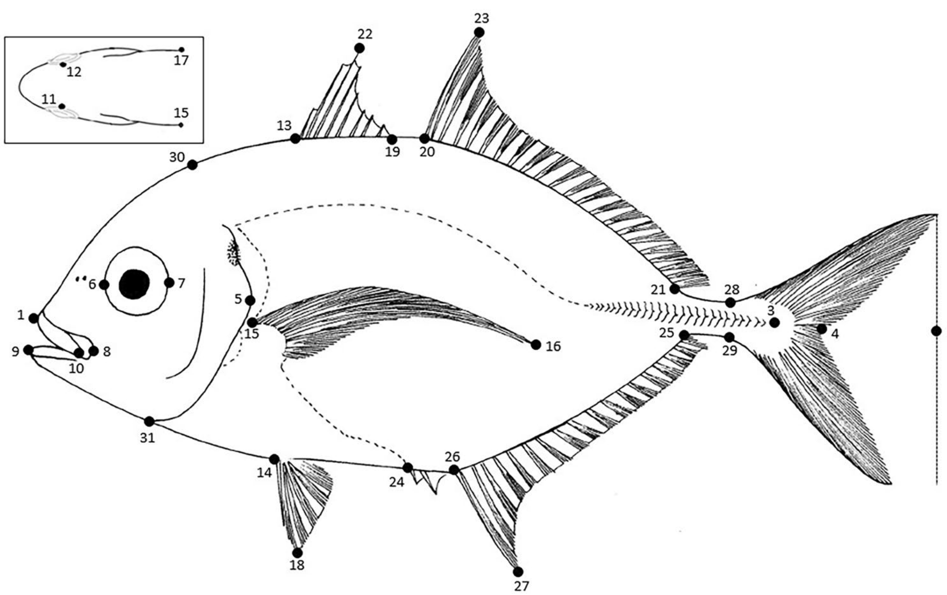

Fig. 2 Landmarks on *Carangoides* spp. for morphometric measurements. Total length (1–2); Standard length (1–3); Fork length (1–4); Head length (1–5); Snout length (1–6); Eye diameter (6–7); Upper jaw length (1–10); Lower jaw length (9–10); Maxillary length (1–8); Postorbital length (7–5); Interorbital length (11–12); Body depth (13–14); Body width (15–17); Pectoral-fin length (15–16); Pelvic-fin length (14–18); Length of first dorsal-fin base (13–19); Length of second dorsal-fin base (20–21); Length of anal-fin base (with two detached spine) (24–25); Length of anal-fin base (without two detached spine) (26–25); Caudal-peduncle length (25–3); Caudal-peduncle depth (28–29); Pre-pelvic length (1–14); Pre-pectoral length (1–15); Pre-dorsal length (1–13); Pre-anal length (1–24)

age groups of each species were used to observe their morphological characteristics. For all dominant species, a minimum of 30 specimens were analysed and for rare species as per availability. Larger fish were measured using measuring tape while smaller fish were measured using digital Vernier calliper to the nearest 0.1 mm. All morphometric measurements were taken from the left lateral aspect. The counting of meristic parameters was done under white light. To increase the accuracy of the counting, a needle was used as an aid to highlight each scale or rays that were counted. All meristic characters were counted twice on the same day by the same observer.

DNA Extraction and Quantification

Total genomic DNA was extracted from the alcohol preserved pectoral fin tissue using salt extraction methods (Miller et al. 1988). The DNA extract was checked for their purities and concentrations using ScanDrop Nano-Volume Spectrophotometer (Analytik Jena) and then stored in 1.5 µL microcentrifuge tubes at -20^{0}C prior to amplification.

Polymerase Chain Reaction (PCR) Amplification and Sequencing

A fragment of 650 base pairs (bp) of COI was amplified using a pair of primers with the sequences 5' TCAACCAAC CACAAAGACATTGGCAC 3' and 5' TAGACTTCTGGG TGGCCAAAGAATCA 3' as forward and reverse primers respectively (Ward et al. 2005). Polymerase reactions were prepared in 25.00 µL reaction volumes comprising of 2.50 µL 10 × PCR buffer, 1.25 µL of $MgCl_2$ (25 mM), 0.60 µL of forward and reverse primers (10 mM), 0.20 µL of *Taq* DNA polymerase (5U/µL) (Vivantis, Malaysia), 0.50 µL dNTP (10 mM/ µL), 2.00 µL 100 ng DNA sample and 17.35 µL double-distilled water (ddH_2O). The thermal regime for COI consisted of an initial step of 95 °C for 2 min (min), and then followed by 40 cycles of 45 s (sec) at 94 °C, 45 s at 50 °C, and 1 min at 72 °C, with a final extension of 10 min at 72 °C. DNA amplification products were separated in 1.2% (w/v) agarose gels at 100 V with 1X Tris–acetate-EDTA (TAE) buffer, stained with SYBR Safe and visualized under UV illumination. Bidirectional sequencing was performed by First BASE Laboratories Sdn. Bhd.

Sequence Editing and Alignment

Initial editing of ambiguous bases was undertaken with MEGA 5 (Molecular Evolutionary Genetics Analysis) software (Tamura et al. 2011). The edited sequences were aligned using ClustalW implemented in the same software. The alignments obtained were further visually checked. Amino acid sequence translation (vertebrate mitochondrial code) was applied and checked for stop codons to ensure the amplification of mitochondrial DNA rather than nuclear copies of COI sequences, and then translated back for subsequent analysis. Initial confirmation of species identification were done by comparing all COI sequences to GenBank (http://blast.ncbi.nlm.nih.gov) (Benson et al. 2013) and BOLD system databases (www.boldsystems.org) (Ratnasingham and Hebert 2007) to avoid misidentification of specimens collected. Similarity thresholds of 97% were used to assign specimens to species level. The aligned sequences have been submitted to the GenBank database under accession numbers MT646199–MT646345. In addition, 124 COI sequences also from Malaysian species of *Carangoides* were retrieved from BOLD Systems (www.boldsystems.org) under project 'DNA Barcoding of Malaysia Marine Fishes' (DBMF), owned by the corresponding author (Table 1) to be included in the DNA analyses.

Molecular Data Analyses

The K2P distance measure was employed to infer the intra- and interspecific nucleotide divergences of Malaysian species of *Carangoides*. The maximum-likelihood (ML) trees were generated using RAxML program based on the HKY + G + I substitution model with 1000 nonparametric bootstrap replicates. *Echeneis naucrates* was used as an outgroup. Automatic Barcode Gap Discovery (ABGD) was also employed for species delimitation analysis (Puillandre et al. 2012) using the online www.abi.snv.jussieu.fr/public/abgd. In order to assess the accuracy of *Carangoides* identification in public databases such as GenBank and BOLD System, a total of 108 COI sequences of *Carangoides* from other regions were retrieved from these public databases.

Results

A total of 589 specimens of *Carangoides* were collected along the coast of Malaysia and all specimens were morphologically identified into 13 species. Diagnostic characters were described in each species in detailed information that present external figures and morphometric and meristic measurements. All the specimens of *Carangoides* have been photographed in fresh specimen where the coloration still exists as shown in Figs. 3 to 15. The current study showed several taxonomic discordances with (Mat Jaafar et al. 2012) (Table 1). This involved the current species assignment to *C. gymnostethus* and *C. coeruleopinnatus* which was previously identified as *C. bajad* and *C. malabaricus,* respectively. Thirteen of the 16 species in Malaysian waters recorded in FishBase (Froese and Pauly 2019) were obtained in this study including three new barcoding records of *C. malabaricus*, *C.*

praeustus and *C. talamparoides* which were failed to collect by Mat Jaafar et al. (2012). The present study shows that *C. oblongus* and *C. talamparoides* are recorded for the first time as specimen-based records while *C. chrysophrys* and *C. fulvoguttatus* are recorded as additional specimen-based distribution records in Malaysian waters.

Identification key to Malaysian *Carangoides*

1a Breast completely scaly 2
1b Breast partially or completely naked 5

2a Second dorsal fin with a black blotch .... *Carangoides praeustus*
2b Second dorsal fin without a black blotch 3

3a Submarginal brown to blackish band present on second dorsal and anal fins (Smith-Vaniz 1999) .... *Carangoides equula*
3b Submarginal band absent on second dorsal and anal fins 4

4a Body with numerous yellow or orange spots; posterior margin of preopercle not black; soft anal-fin rays 21 to 23 (mainly 22); scutes 21 to 25 .... *Carangoides bajad*
4b Body without yellow or orange spots or if present, only a few small yellow spots; posterior margin of preopercle black; soft anal-fin rays 18 to 20; scutes 11 to 18 (Smith-Vaniz 1999) .... *Carangoides plagiotaenia*

5a Soft dorsal-fin rays 26 to 32; soft anal-fin rays 21 to 26 6
5b Soft dorsal-fin rays 17 to 23; soft anal-fin rays 15 to 19 9

6a Breast naked ventrally to insertion of pelvic fin 7
6b Breast naked ventrally to behind insertion of pelvic fin 8

7a Body with lateral dusky bands without spots or if present, small and numerous yellow or orange spots; total gill rakers including rudiments on first gill arch 27 to 28 (mainly 27) .... *Carangoides ferdau*
7b Body without lateral dusky bands with large yellow spots present mostly below lateral line; total gill rakers including rudiments on first gill arch 28 to 32 (Smith-Vaniz 1999) .... *Carangoides orthogrammus*

8a Mouth cleft located at the level with the lower margin of the eye; total gill rakers including rudiments on first gill arch 28 to 30 (mainly 29); soft dorsal-fin rays 29 to 31 (mainly 30) .... *Carangoides gymnostethus*
8b Mouth cleft located below the lower margin of the eye; total gill rakers including rudiments on first gill arch 24 to 27 (mainly 26); soft dorsal-fin rays 26 to 28 (mainly 28) .... *Carangoides fulvoguttatus*

9a Naked area of breast separated from naked base of pectoral fin by a moderate to narrow band of scales 10
9b Naked area of breast extended to naked base of pectoral fin 11

10a Curved part of lateral line slightly longer than straight part; soft dorsal-fin rays 17 to 19 (mainly 18); soft anal-fin rays 16 to 17 (mainly 17); scutes 26 to 32 .... *Carangoides dinema*
10b Curved part of lateral line slightly shorter than straight part; soft dorsal-fin rays 20 to 22 (mainly 21); soft anal-fin rays 18 to 19 (mainly 18); scutes 40 to 44 .... *Carangoides oblongus*

11a Small naked area presents just above pectoral-fin base 12
11b Small naked area absents above pectoral-fin base 13

12a Tongue yellowish to dark brown that densely pigmented with brown to greyish brown chromatophores; total gill rakers including rudiments on first gill arch 31 to 37 (mainly 34) .... *Carangoides malabaricus*
12b Tongue whitish to pale grey that sparsely pigmented with pale grey chromatophores; total gill rakers including rudiments on first gill arch 28 to 32 (mainly 29) .... *Carangoides talamparoides*

13a Total gill rakers including rudiments on first gill arch 34 to 37 .... *Carangoides armatus*
13b Total gill rakers including rudiments on first gill arch 21 to 25 14

14a Head profile with a distinct break or "bump" in the interorbital region .... *Carangoides hedlandensis*
14b Head profile without a distinct break or "bump" in the interorbital region 15

15a Snout abruptly vertical above mouth cleft; soft dorsal-fin rays 18 to 20 (mainly 20) .... *Carangoides chrysophrys*

15b Snout not abruptly vertical above mouth cleft; soft dorsal-fin rays 21 to 23 (mainly 22) .... *Carangoides coeruleopinnatus*

Taxonomy

Carangoides armatus (Forsskål 1775)
(English name: Longfin Trevally)
(Local name: Demuduk Putih)
(Fig. 3; Table 2)

Sciaena armata Forsskål in Niebuhr 1775: 53 (type locality: Red Sea; no types known).

Carangoides armatus – Mansor et al. 1998: 141; Annie and Albert 2009: 136; Ambak et al. 2010: 119; Atan et al. 2010: 36e (Pulau Pinang); Kimura et al. 2015: 44; Ahmad et al. 2018: 84.

Material examined CA01–CA04, CA06–CA14, CA17–CA30, SB53, SB54, SB65, SB99.

Diagnosis Dorsal-fin rays VIII + I, 19–21 (mainly 20); anal-fin rays II + I, 17–18 (17). Lateral-line scales 72–89; lateral-line scutes 14–21; total elements on straight part of lateral line 31–42. Gill rakers 12–14 (13) + 21–24 (23) = 34–37 (36). Body oval, deep and strongly compressed. Dorsal contour of head almost straight from snout to nape. Snout pointed. Breast naked ventrally to behind the insertion of pelvic fin; laterally naked area of breast extends to naked base of pectoral fin. Second dorsal and anal-fins lobe elongate and filamentous. Middle rays of second dorsal and anal fins produced long filaments in matured males, weakly develops in young and female.

Coloration Body silvery blue dorsally and silvery to white ventrally. Small dark spot on upper margin of operculum.

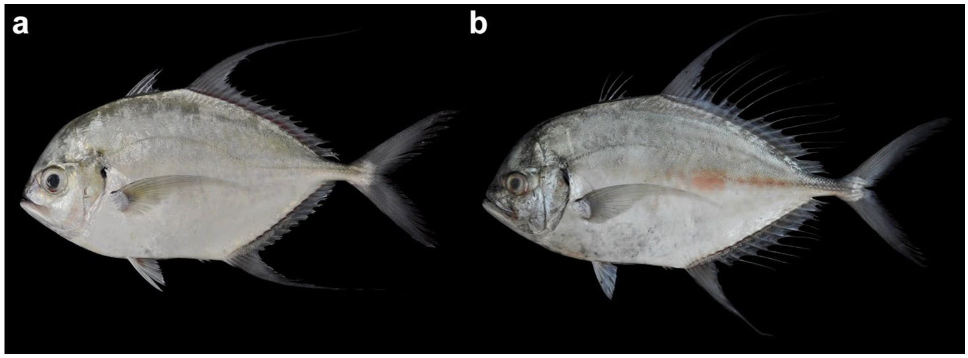

Fig. 3 *Carangoides armatus*. **a** subadult, UMTF9389, 24.0 cm SL; **b** adult, UMTF9392, 40.0 cm SL

Size Largest specimen examined 445 mm fork length. The maximum recorded size by FAO for this species is 500 mm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Western Indian Ocean from South Africa northward to southern India and Sri Lanka, including the Red Sea, Gulf of Oman, and west coast of Malagasy Republic; in the western Pacific known from the Gulf of Thailand, Hong Kong, Thailand, Okinawa, and Japan.

Remarks *Carangoides armatus* is the most similar in general appearance to *C. hedlandensis*. However, its head profile is relatively straight from nape to snout. The first photographic record of *C. armatus* from Malaysia was based solely on misidentification of *C. hedlandensis* by Mohsin and Ambak (1996); and Smith-Vaniz (1999) also not include its occurrence in Malaysian waters. However, more photographic evidences were reported and showed *C.armatus* is common and widely distributed in Malaysia waters. However, we have not yet found any occurrence from Celebes Sea.

Carangoides bajad (Fabricius 1775)
(English name: Orange-spotted Trevally)
(Local name: Demuduk Bintik Oren)
(Fig. 4; Table 2)

Scomber ferdau var. *bajad* Fabricius 1775: 55 (type locality: Red Sea; syntypes: ZMUC P46437-438).

Carangoides bajad – Mohsin and Ambak 1996: 427, 727, Fig. 328; Mansor et al. 1998: 141; Annie and Albert 2009: 137; Ambak et al. 2010: 120; Atan et al. 2010: 36f (Terengganu).

Material examined CB01, CB02, CB03, SB27, SB28.

Diagnosis Dorsal-fin rays VIII + I, 24–26 (mainly 25); anal-fin rays II + I, 21–23 (22). Lateral-line scales 98–118; lateral-line scutes 21–25; total elements on straight part of lateral line 45–52. Gill rakers 7–8 (8) + 20–21 (20) = 28–29 (28). Body oblong and slightly compressed. Dorsal profile of head almost straight. Snout blunt. Breast completely scaled. No filamentous rays on dorsal and anal fins. Pectoral fins falcate and long, reaching straight parts of lateral line.

Coloration Body bluish grey dorsally, white to yellowish ventrally. Numerous yellow to orange spots scattered on both sides of body. Caudal, soft dorsal and soft anal fin greyish yellow. Pectoral and pelvic fins pale greyish yellow to hyaline. Capable of rapidly changing color to overall orange.

Size Largest specimen examined 490 mm total length. The maximum recorded size by FAO for this species is 550 mm total length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widely distributed in Indian oceans from the Red Sea, Gulf of Aden, Persian Gulf, and the Gulf of Oman; Indo-West Pacific known from the Gulf of Thailand, Okinawa, Indonesia, Philippines, and New Britain.

Remarks Distinctive species that can be easily distinguished from other *Carangoides* species by a combination of characters: breast completely scaly and sides of body covered by numerous yellow or orange spots.

Carangoides chrysophrys (Cuvier 1833)
(English name: Longnose Trevally)
(Local name: Demuduk Muncung)
(Fig. 5; Table 2)

Fig. 4 *Carangoides bajad,* UMTF9398, 24.5 cm SL

Table 2 Selected characters in Malaysian species of *Carangoides*

Species	Breast squamation	Gill rakers (upper + lower = total)	Dorsal-fin rays	Anal-fin rays	Straight LL (scales + scute)
C. armatus	Naked ventrally to behind origin of pelvic fin; laterally to naked base of pectoral fin	12–14 (13) + 21–24 (23) = 34–37 (36)	VIII + I, 19–21 (20)	II + I, 17–18 (17)	31–42 + 14–21
C. bajad	Breast completely scaly	7–8 (8) + 20–21 (20) = 28–29 (28)	VIII + I, 24–26 (25)	II + I, 21–23 (22)	45–52 + 21–25
C. chrysophrys	Naked ventrally to behind origin of pelvic fin; laterally, extends diagonally to naked base of pectoral fin but does not extend above it	6–8 (6) + 15–18 (17) = 22–25 (23)	VIII + I, 18–20 (20)	II + I, 15–17 (16)	34–42 + 20–29
C. coeruleopinnatus	Naked ventrally to distinctly behind origin of pelvic fin; laterally, naked area of breast extends to naked based of pectoral fin, but not include small area just above pectoral-fin base	6–8 (7) + 15–18 (16) = 21–25 (23)	VIII + I, 21–23 (22)	II + I, 17–19 (18)	33–42 + 16–20
C. dinema	Naked area of breast separated from naked base of pectoral fin by a moderate to narrow band of scale	7–9 (8) + 16–19 (18) = 23–28 (26)	VIII + I, 17–19 (18)	II + I, 16–17 (17)	27–34 + 26–32
C. ferdau	Naked ventrally to origin of pelvic fins; laterally naked area of breast separated from naked base of pectoral fin by a moderate band of scales	8–9 (8) + 19 = 27–28 (27)	VIII + I, 29–32 (32)	II + I, 25–26 (25)	47–57 + 26–31
C. fulvoguttatus	Naked ventrally to behind the insertion of pelvic fin; laterally naked area of breast extends to naked base of pectoral fin or separated by a moderate to very narrow band of scales	6–8 (7) + 17–22 (18) = 24–27 (26)	VIII + I, 26–28 (28)	II + I, 21–25 (23)	35–46 + 15–25
C. gymnostethus	Naked ventrally to behind the insertion of pelvic fin; laterally naked area of breast extends to naked base of pectoral fin	8–9 (8) + 19–22 (21) = 28–30 (29)	VIII + I, 29–31 (30)	II + I, 23–26 (25)	42–48 + 23–31
C. hedlandensis	Naked ventrally to behind the insertion of pelvic fin; laterally naked area of breast extends to naked base of pectoral fin	6–9 (8) + 15–17 (16) = 22–25 (24)	VIII + I, 20–22 (21)	II + I, 16–18 (17)	31–42 + 18–29
C. malabaricus	Naked ventrally to distinctly behind origin of pelvic fin, often extending to anal spine; laterally, naked area of breast extends to naked based of pectoral fin, including small area present just above pectoral-fin base	9–11 (10) + 21–27 (25) = 31–37 (34)	VIII + I, 20–23 (22)	II + I, 17–19 (18)	32–42 + 23–34
C. oblongus	Naked ventrally to insertion of pelvic fins; laterally, naked area of breast separated from naked base of pectoral fin by a moderate to narrow band of scale	8–10 (9) + 18–20 (19) = 26–30 (29)	VIII + I, 20–22 (21)	II + I, 18–19 (18)	41–47 + 40–44

Table 2 (continued)

Species	Breast squamation	Gill rakers (upper + lower = total)	Dorsal-fin rays	Anal-fin rays	Straight LL (scales + scute)
C. praeustus	Breast completely scaly	10–11 (10) + 23–25 (24) = 33–35 (35)	VIII + I, 21–23 (23)	II + I, 18–19 (19)	31–37 + 24–29
C. talamparoides	Naked ventrally to distinctly behind origin of pelvic fin, often extending to anal spine; laterally, naked area of breast extends to naked based of pectoral fin, including small area present just above pectoral-fin base	7–9 (8) + 21–23 (21) = 28–32 (29)	VIII + I, 21–23 (22)	II + I, 17–19 (18)	30–37 + 21–31

() Most frequent number of counting

Caranx chrysophrys Cuvier in Cuvier and Valenciennes 1833: 77 (type locality: Seychelles; holotype: MNHN A-0560).

Carangoides chrysophrys – Mansor et al. 1998: 142; Annie and Albert 2009: 138; Ambak et al. 2010: 120; Atan et al. 2010: 37b (Terengganu); Ahmad et al. 2018: 85; Seah et al. 2020: 49.

Material examined CCR01–CCR07, CCR09–CCR13, CCR16–CCR24, CCR28–CCR34, SB97, SB98, SB118, SB119, SB120, SB125, SB142, SB150, SB151, SB152.

Diagnosis Dorsal-fin rays VIII + I, 18–20 (mainly 20); anal-fin rays II + I, 15–17 (16). Lateral line scales 80–103; lateral-line scutes 20–29; total elements on straight part of lateral line 34–42. Gill rakers 6–8 (6) + 15–18 (17) = 22–25 (23). Body strongly compressed, sub-ovate in juveniles, oblong in adults. Head profile convex, gently sloped, then abruptly vertical at tip of snout. Breast naked ventrally up to pectoral fin base and until behind insertion of pelvic fin. Anterior second dorsal and anal fins elongated in juvenile and sub-adult.

Coloration Body silvery blue dorsally, silvery white ventrally. Opercle with small black spot on upper margin. Dorsal and anal fins whitish to pale yellow and dusky. White spots at the base of anal-fin membranes. Caudal and pectoral fins pale to dusky yellow.

Fig. 5 *Carangoides chrysophrys*, UMTF9450, 18.0 cm SL

Size Largest specimen examined 360 mm fork length. The maximum recorded size by FAO for this species is 385 mm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widespread in Indo-west Pacific Ocean, from Okinawa to Australia and eastward to New Britain. Also occur in coastal waters of the Indian Ocean, including the Red Sea and Persian Gulf.

Remarks *Carangoides chrysophrys* may be distinguished from other Malaysia *Carangoides* species in having the snout abruptly vertical above the mouth cleft in adults. This species can be distinguished from *C. malabaricus* and *C. talamparoides* by the combination of lower counts of gill rakers, dorsal-fin and anal-fin rays and having scaly area above pectoral-fin base (vs. naked for *C. malabaricus* and *C. talamparoides*). The present study provides additional specimen-based distribution records of *C. chrysophrys* occurences in the east coast of Peninsular Malaysia.

Carangoides coeruleopinnatus (Rüppell 1830)
(English name: Coastal Trevally)
(Local name: Demuduk Cupak)
(Fig. 6a, b; Table 2)

Caranx coeruleopinnatus Rüppell 1830: 100 (type locality: Red Sea, Saudi Arabia, Jeddah; lectotype: SMF 2873)

Carangoides caeruleopinnatus – Annie and Albert 2009: 137; Ambak et al. 2010: 120; Atan et al. 2010: 37a (Terengganu); Ahmad et al. 2018: 83

Carangoides coeruleopinnatus – Matsunuma et al. 2011: 101; Seah et al. 2020: 50

Carangoides uii – Mansor et al. 1998: 146

Material examined CC01–CC29, CC40–CC44, CC46–CC49, CC56–CC58, CC63–CC65, CC69–CC71, CC74, CC75, CC77–CC80, CC89–CC96, SB12, SB13,

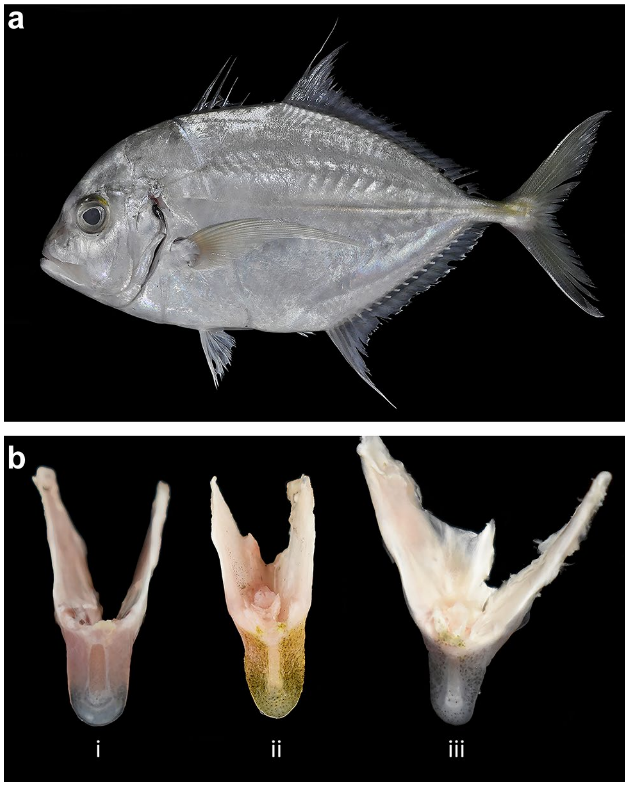

Fig. 6 **a** *Carangoides coeruleopinnatus*, UMTF9407, 23.0 cm SL, **b** Tongue color and appearance: (i) *C. coeruleopinnatus,* UMTF9440, 11.4 cm SL; (ii) *C. malabaricus,* UMTF9519, 13.3 cm SL; and (iii) *C. talamparoides,* UMTF9534, 13.3 cm SL

SB30, SB31, SB51, SB57, SB61, SB62, SB73, SB74, SB75, SB94, SB95, SB96, SB112, SB113, SB136, SB137, SB138, SB139, SB165, SB167, SB168.

Diagnosis Dorsal-fin rays VIII + I, 21–23 (mainly 22); anal-fin rays II + I, 17–19 (18). Lateral-line scales 80–100; lateral-line scutes 16–20; total elements on straight part of lateral line 33–42. Gill rakers 6–8 (7) + 15–18 (16) = 21–25 (23). Body strongly compressed, almost ovate. Nape moderately curved. Snout pointed. Breast naked ventrally to distinctly behind origin of pelvic fin; laterally, naked area of breast extends to naked based of pectoral fin, but not include small area just above pectoral fin base. Anterior second dorsal and anal fins elongated in juvenile and sub-adult.

Coloration Body silvery blue dorsally and silvery white on sides and ventrally. Sometimes with numerous small yellow spots laterally. A small black spot on upper margin of operculum. Tongue white. Soft dorsal, soft anal and caudal fins dusky, with white spots at the base of anal fin membranes.

Size Largest specimen examined 284 mm fork length. The maximum recorded size by FAO for this species is 360 mm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widespread in Indo-west Pacific Ocean throughout the eastern Indian and western Pacific oceans from Japan to Australia.

Remarks *Carangoides coeruleopinnatus* are very similar to another two Malaysian *Carangoides* species, *C. malabaricus* and *C. talamparoides* in general body shape and coloration. *Carangoides malabaricus* and *C. talamparoides* may be distinguished from *C. coeruleopinnatus* on the basis of breast squamation (naked area on breast extends above pectoral base in *C. malabaricus* and *C. talamparoides*; does not in *C. coeruleopinnatus*) and gill raker counts (9–11 + 21–27 = 31–37 for *C. malabaricus*; 7–9 + 21–23 = 28–32 for *C. talamparoides*; 6–8 + 15–18 = 21–25 for *C. coeruleopinnatus*). Tongue color and dentition also can be used to distinguish these three species. *Carangoides malabaricus* has yellow to dark brown tongue compared to white in *C. coeruleopinnatus* and *C. talamparoides* (Fig. 6b). However, *C. coeruleopinnatus* and *C. talamparoides* can be distinguished through tongue dentition (in the form of broad, square-ended villiform band in *C. coeruleopinnatus* and narrow, round-ended villiform band in *C. talamparoides*). All previous Malaysian literature records except Matsunuma et al. (2011) and Seah et al. (2020) had misspelled *C. coeruleopinnatus* as *C. caeruleopinnatus*.

Carangoides dinema (Bleeker 1851)
(English name: Shadow Trevally)
(Local name: Demuduk Bayang)
(Fig. 7; Table 2)

Carangoides dinema Bleeker 1851: 365 (type locality: Jakarta, Java, Indonesia; no types known).

Carangoides dinema – Mohsin and Ambak 1996: 427, 727, Fig. 326; Mansor et al. 1998: 142; Ambak et al. 2010: 121; Atan et al. 2010: 37c (Sabah).

Fig. 7 *Carangoides dinema*, UMTF9462, 15.0 cm SL

Material examined CD01–CD07, CD09, SB16, SB17, SB18, SB19, SB32, SB33, SB49, SB55, SB68, SB69, SB70, SB85, SB86, SB87, SB88, SB89, SB90.

Diagnosis Dorsal-fin rays VIII + I, 17–19 (mainly 18); anal-fin rays II + I, 16–17 (17). Lateral-line scales 54–60; lateral-line scutes 26–32; total elements on straight part of lateral line 27–34. Gill rakers 7–9 (8) + 16–19 (18) = 23–28 (26). Body almost ovate and compressed. Head triangular, pointed anteriorly. Nape slightly elevated and almost straight. Snout pointed. Breast naked ventrally to insertion of pelvic fins; laterally, naked area of breast separated from naked base of pectoral fin by a moderate to narrow band of scales. Anterior second dorsal and anal fins lobe elongate and filamentous.

Coloration Body silvery blue dorsally and silvery white ventrally. Small black blotches (becoming larger posteriorly) on back at the base of second dorsal-fin rays. Dorsal and caudal fins pale to dusky. Pectoral fin hyaline. Pelvic and anal fins whitish to dusky.

Size Largest specimen examined 276 mm fork length. The maximum recorded size by FAO for this species is 530 mm fork length.

Distribution Malaysia: Widespread in Sabah and rarely found in Sarawak. No record from Peninsular Malaysia. General: Broadly distributed throughout the Indo-West Pacific Ocean known from southern Japan, Okinawa, Indonesia, Philippines, Papua New Guinea, Tonga Islands, and Samoa. In the Indian Ocean known only from South Africa to Tanzania.

Remarks *Carangoides dinema* is most similar to *C. oblongus* in general appearance. However, it can be distinguished by having 26–32 lateral-line scutes (41–44 in *C. oblongus*), straight part of lateral line slightly shorter than curved part (straight part of lateral line slightly longer than curved part in *C. oblongus*) and 17–19 soft dorsal fin rays (20–22 in *C. oblongus*).

Carangoides ferdau (Fabricius 1775)
(English name: Blue Trevally)
(Local name: Demuduk Biru)
(Fig. 8; Table 2)

Scomber ferdau Fabricius in Niebuhr 1775: 55 (type locality: Red Sea, Saudi Arabia, Jeddah; Forsskål specimens: ZMUC P46442).

Carangoides ferdau – Mohsin and Ambak 1996: 428, 727, Fig. 327; Mansor et al. 1998: 143; Ambak et al. 2010: 121; Atan et al. 2010: 37e (Pulau Pinang).

Material examined CF01, CF02, CF03, CF04, SB14, SB92.

Diagnosis Dorsal-fin rays VIII + I, 29–32 (mainly 32); anal-fin rays II + I, 25–26 (25). Lateral-line scales 95–114; lateral-line scutes 26–31; total elements on straight part of lateral line 47–57. Gill rakers 8–9 (8) + 19 = 27–28 (27). Body ovate to elongate-ovate and slightly compressed. Dorsal part of the head gently sloping and more convex than ventral profile. Snout bluntly rounded. Breast naked ventrally to origin of pelvic fins; laterally naked area of breast separated from naked base of pectoral fin by a moderate band of scales. Anterior second dorsal and anal fins lobe elongate and filamentous.

Fig. 8 *Carangoides ferdau*, UMTF9465, 15.4 cm SL

Coloration Body silvery blue dorsally and white to pale greyish ventrally, shading to silvery on sides with six to seven dusky bands laterally. Soft dorsal and anal fins whitish to dusky. Pectoral fins proximal yellowish to dusky. Caudal fin dusky.

Size Largest specimen examined 200 mm fork length. The maximum recorded size by FAO for this species is 470 mm fork length.

Distribution Rarely found in Peninsular Malaysia and Sabah. General: Widespread from the Red Sea and east coast of Africa to Hawaiian Islands and French Polynesia; in the western Pacific from Australia (Great Barrier Reef) to southern Japan.

Remarks *Carangoides ferdau* can be easily distinguish from other *Carangoides* species based on external morphology except for *Carangoides orthogrammus* (not found in this study). The most reliable characters that can be used to distinguish between the species are coloration. *C. orthogrammus* has two to seven large, yellow spots with yellow borders on the sides of the body, and usually has no dusky vertical bars on the sides (Smith-Vaniz 1999); in *C. ferdau* yellow or orange spots are usually absent or, if present, are small and numerous and adults typically have five to seven relatively broad, dusky vertical bars on the sides of the body. Present study extending the known distribution of this species to northwestern Peninsular Malaysia.

Carangoides fulvoguttatus (Forsskål 1775)
(English name: Yellowspotted Trevally)
(Local name: Demuduk Bintik Kuning)
(Fig. 9; Table 2)

Scomber fulvoguttatus Forsskål 1775: 56 (type locality: Red Sea; no types known).

Carangoides fulvoguttatus – Mansor et al. 1998: 143; Chin 1998: 57; Ambak et al. 2010: 121; Atan et al. 2010: 37f.

Material examined CFV04–CFV22, SB29, SB47, SB60, SB64.

Diagnosis Dorsal-fin rays VIII + I, 26–28 (mainly 28); anal-fin rays II + I, 21–25 (23). Lateral-line scales 97–119; lateral-line scutes 15–25; total elements on straight part of lateral line 35–46. Gill rakers 6–8 (7) + 17–22 (18) = 24–27 (26). Body oblong and compressed in juvenile, becoming elongate and sub-cylindrical in adult. Head profile and nape convex becoming more steep with age. Snout bluntly rounded. Mouth cleft distinctly below level of eye. Breast naked ventrally to behind the insertion of pelvic fin; laterally naked area of breast extends to naked base of pectoral fin or separated by a moderate to very narrow band of scales. No filamentous rays on dorsal and anal fins.

Coloration Body bluish green dorsally and silvery white ventrally with many yellow to golden spots on upper two thirds of body and four to five bands laterally (sometimes indistinct or absent). Opercular spot dusky. Dorsal, anal and caudal fins dusky yellow. Soft dorsal and soft anal fins tip white to yellow.

Size Largest specimen examined 600 mm total length. The maximum recorded size is 10 kg, spearfishing record from South Africa. Reported to attain 100 cm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widely distributed through the Indian and western Pacific oceans, including Okinawa, Palau, and Australia.

Remarks *C. fulvoguttatus* are very similar to *C. gymnostethus* in general body shape and coloration. However *C. fulvoguttatus* can be clearly distinguished from *C. gymnostethus* by the location of the mouth cleft. In *C. fulvoguttatus*, the mouth cleft located below the lower margin of the eye; in *C. gymnostethus* mouth cleft located at the level with the lower margin of the eye. Other character separating the species are gill rakers and soft dorsal-fin rays count. In *C. fulvoguttatus*, total number of gill rakers 24–27 and soft dorsal-fin rays 26–28; in *C. gymnostethus*, total number of gill rakers 28–30 and soft dorsal-fin rays 29–31. Present study provides the additional specimen-based distribution records of its occurrences in the Straits of Malacca, Sulu Sea and Celebes Sea. This species is common and widely distributed in Malaysia waters.

Fig. 9 *Carangoides fulvoguttatus*, UMTF9474, 27.0 cm SL

Carangoides gymnostethus (Cuvier 1833)
(English name: Bludger Trevally)
(Local name: Demuduk Nyiur-nyiur)
(Fig. 10; Table 2)

Caranx gymnostethus Cuvier in Cuvier and Valenciennes 1833: 73 (type locality: Seychelles, western Indian Ocean; holotype: MNHN A-5582).

Carangoides gymnostethus – Mohsin and Ambak 1996: 428, 727, Fig. 325; Mansor et al. 1998: 143, 144; Ambak et al. 2010: 121; Atan et al. 2010: 38a (Terengganu); Matsunuma et al. 2011: 101; Ahmad et al. 2018: 85.

Material examined CG01–CG19, CG21, SB20, SB46, SB66, SB67, SB91, SB109, SB110, SB111 SB140, SB141, SB148, SB161**.**

Diagnosis Dorsal-fin rays VIII + I, 29–31 (mainly 30); anal-fin rays II + I, 23–26 (25). Lateral-line scales 93–127; lateral-line scutes 23–31; total elements on straight part of lateral line 42–48. Gill rakers 8–9 (8) + 19–22 (21) = 28–30 (29). Body ovate, deep, compressed in young; becoming elongate and sub-cylindrical with growth. Dorsal profile of head and nape slightly convex. Snout bluntly rounded. Mouth cleft at level with lower margin of eye in adults. Breast naked ventrally to behind insertion of pelvic fins, lateral naked area extending to pectoral fin base. No filamentous rays on dorsal and anal fins.

Coloration Body bluish green to dusky dorsally and silvery white ventrally. A few brown to yellow spots sometimes midlaterally on body. Opercular spot absent or dusky.

Fig. 10 *Carangoides gymnostethus*, UMTF9478, 28.2 cm SL

Dorsal, anal and caudal fins dusky. Anterior edge and distal margin of anal fin white. Pectoral and pelvic fins hyaline.

Size Largest specimen examined 470 mm total length. The maximum recorded size is 14.5 kg, spearfishing record from South Africa. Reported to attain at least 900 mm total length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widely distributed in tropical and subtropical waters of the Indo-Pacific.

Remarks See *C. fulvoguttatus* for comparison with *C. gymnostethus.*

Carangoides hedlandensis (Whitley 1934)
(English name: Bumpnose Trevally)
(Local name: Demuduk Lekuk)
(Fig. 11; Table 2)

Olistus hedlandensis Whitley 1934: 156 (type locality: Port Hedland, Western Australia; holotype: AMS I.12957).

Carangoides armatus (non Rüppell) – Mohsin and Ambak 1996: 426, 727, Fig. 324.

Carangoides hedlandensis – Mansor et al. 1998: 144; Annie and Albert 2009: 139; Ambak et al. 2010: 122; Atan et al. 2010: 38b (Sabah); Matsunuma et al. 2011: 102; Ahmad et al. 2018: 84; Seah et al. 2020: 50.

Material examined CH01–CH29, CH35–CH37, SB10, SB11, SB38, SB48, SB59, SB63, SB82, SB83, SB93, SB108, SB121–SB124, SB132–SB135, SB143, SB144, SB153–SB157, SB162–SB164.

Diagnosis Dorsal-fin rays VIII + I, 20–22 (mainly 21); anal-fin rays II + I, 16–18 (17). Lateral-line scales 71–98; lateral-line scutes 18–29; total elements on straight part of lateral line 31–42. Gill rakers 6–9 (8) + 15–17 (16) = 22–25 (24). Body strongly compressed and deep. Head profile convex with a bump on interorbital region. Snout pointed. Breast naked to pectoral-fin base and behind insertion of pelvic fin. Anterior rays of dorsal and anal fins extending into long filaments. Second dorsal and anal fin rays produced filaments in adult male.

Coloration Body silvery to bluish grey dorsally and silvery white ventrally with 5–6 dark bands in juvenile. A black spot on upper margin of opercle. Anterior rays of soft dorsal fin and distal portions of dorsal filaments darker. Anal-fin rays and filaments white. Caudal fin yellowish to dusky.

Size Largest specimen examined 288 mm fork length. The maximum recorded size is 283 mm, an holotype of *Olistus malabaricus* (a synonym of *C. hedlandensis*) from Malabar, India.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Indo West Pacific: East Africa, South Africa, Seychelles and Réunion (Mascarenes) east to Philippines, Indonesia, southern India and Sri Lanka, Bay of Bengal, Gulf of Thailand, Taiwan province of China, Okinawa, Japan, Australia, New Guinea and Samoa and Tonga.

Remarks A steep head profile with the distinct break ("bump") in the interorbital region and the elongated of the soft dorsal and soft anal fin rays in matured males distinguished *C. hedlandensis* from other Malaysian *Carangoides* species.

Carangoides malabaricus (Bloch and Schneider 1801)
(English name: Malabar Trevally)
(Local name: Demuduk Cermin)
(Fig. 12; Table 2)

Scomber malabaricus Bloch and Schneider 1801: 31 (type locality: India, Tranquebariam [Tharangambadi]; holotype: ZMB 8760).

Carangoides malabaricus – Mohsin and Ambak 1996: 430, 727, Fig. 329; Mansor et al. 1998: 144; Annie and Albert 2009: 139; Ambak et al. 2010: 122; Atan et al. 2010:

Fig. 11 *Carangoides hedlandensis,* UMTF9494, 12.2 cm SL

Fig. 12 *Carangoides malabaricus*, UMTF9508, 14.1 cm SL

38c (Pulau Pinang); Matsunuma et al. 2011: 102; Ahmad et al. 2018: 83.

Material examined CM02–CM22, CM25–CM32, SB22, SB50, SB76, SB77, SB79, SB80, SB81, SB100, SB101, SB102, SB115, SB116, SB117, SB 128, SB129, SB 130, SB 131, SB145, SB158, SB159, SB160, SB170, SB172, SB173.

Diagnosis Dorsal-fin rays VIII + I, 20–23 (mainly 22); anal-fin rays II + I, 17–19 (18). Lateral-line scales 65–77; lateral-line scutes 23–34; total elements on straight part of lateral line 32–42. Gill rakers 9–11 (10) + 21–27 (25) = 31–37 (34). Body ovate and strongly compressed. Dorsal profile more convex than ventral profile. Snout pointed. Naked area of breast wide, extending dorsally beyond pectoral-fin base, including small area anteriorly just above pectoral-fin base and ventrally beyond insertion of pelvic fins, usually extending to anal fin origin. No filamentous rays on dorsal and anal fins.

Coloration Body silvery blue dorsally and silvery white ventrally. A small black spot on upper margin of operculum. Caudal, soft dorsal and soft anal fin whitish to yellow. White spots at the base of anal-fin membranes. Tongue yellowish to brown.

Size Largest specimen examined 209 mm fork length. The maximum recorded size by FAO for this species is 240 mm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widespread in Indo-west Pacific Ocean, from Straits of Malacca, Gulf of Thailand, Okinawa Japan, Indonesia and Australia. Western Indian ocean—from South Africa to Sri Lanka, including the west coast of the Malagasy Republic.

Remarks *Carangoides malabaricus* may be easily confused with the similar *C. talamparoides*. Previous studies (Kluzinger 1871; Williams and Venkataramani 1978; Gunn 1990; Bogorodsky et al. 2017) have discussed and describe the morphology similarity of these two species. From the previous study and also through this study, the most important diagnostic character to differentiate these two species are gill raker counts (9–11 + 21–27 = 31–37 for *C. malabaricus*; 7–9 + 21–23 = 28–32 for *C. talamparoides*). Williams and Venkataramani (1978) have used two addditional characters to distinguish *C. malabaricus* from *C. talamparoides* which are snout length and pre-dorsal distance.

Carangoides oblongus (Cuvier 1833)
(English name: Coachwhip Trevally)
(Local name: Demuduk Letup-Letup)
(Fig. 13; Table 2)

Caranx oblongus Cuvier in Cuvier and Valenciennes 1833: 128 (type locality: New Guinea; holotype: MNHN A-6172).

Fig. 13 *Carangoides oblongus,* UMTF9521, 16.4 cm SL

Carangoides oblongus – Annie and Albert 2009: 140.

Material examined CO01, CO02, SB34, SB35, SB36, SB56, SB71, SB103.

Diagnosis Dorsal-fin rays VIII + I, 20–22 (mainly 21); anal-fin rays II + I, 18–19 (18). Lateral-line scales 55–60; lateral-line scutes 40–44; total elements on straight part of lateral line 41–47. Gill rakers 8–10 (9) + 18–20 (19) = 26–30 (29). Body almost ovate, oblong and compressed. Head profile gently convex. Snout pointed. Breast naked ventrally to insertion of pelvic fins; laterally, naked area of breast separated from naked base of pectoral fin by a moderate to narrow band of scale. Anterior second dorsal and anal-fins lobe elongate and filamentous. Straight part of lateral line longer than curved part with strong scutes.

Coloration Body silvery blue dorsally and silvery white ventrally. No opercular spot. Upper caudal-fin lobe and soft dorsal dusky. Lower caudal fin and soft anal fin yellowish. Pectoral fins proximal yellowish.

Size Largest specimen examined 288 mm fork length. The maximum recorded size by FAO for this species is 410 mm fork length.

Distribution Malaysia: Widespread in Sabah and rarely found in Sarawak and Peninsular Malaysia. General: Broadly distributed throughout the Indo-West Pacific Ocean known from Thailand, Japan, Indonesia, the Philippines, Palau, New Britain, Australia, Papua New Guinea, Solomon Islands and Fiji.

Remarks *Carangoides oblongus* may be easily distinguished from other Malaysian *Carangoides* species by its strong scutes. In other species, scute range from feeble to moderate and generally the number fewer than 40. See *C. dinema* for comparison with *C. oblongus.* Present study provides the first specimen-based records of its occurrences in Malaysia waters. This species is rare species and we have not yet found any occurrence from east coast of Peninsular Malaysia.

Carangoides praeustus (Anonymous [Bennett] 1830)
(English name: Brownback Trevally)
(Local name: Demuduk Abu-Abu)
(Fig. 14; Table 2)

Caranx praeustus Anonymous [Bennett] 1830: 689 (type locality: Sumatra, Indonesia; no types known).

Carangoides praeustus – Mohsin and Ambak 1996: 431, 729, Fig. 331; Annie and Albert 2009: 140; Ambak et al. 2010: 123; Atan et al. 2010: 38 g; Ahmad et al. 2018: 82.

Material examined SB01–SB09, SB15, SB52.

Diagnosis Dorsal-fin rays VIII + I, 21–23 (mainly 23); anal-fin rays II + I, 18–19 (19). Lateral-line scales 59–64; lateral-line scutes 24–29; total elements on straight part of lateral line 31–37. Gill rakers 10–11 (10) + 23–25 (24) = 33–35 (35). Body elongate and compressed. Dorsal and ventral profile equally convex. Head dorsal profile nearly straight. Snout pointed. Breast completely scaly. No filamentous rays on dorsal and anal fins. Curved part of lateral line longer than straight part.

Coloration Body silvery blue dorsally and silvery white ventrally. No black spot on opercular. Second dorsal fin pale dusky with a black blotch. Caudal fin yellowish. Anal fin, pectoral fin and pelvic fin hyaline to whitish.

Size Largest specimen examined 166 mm fork length. The maximum recorded size by FAO for this species is 195 mm fork length.

Distribution Malaysia: Widespread in Sabah. No record from Peninsular Malaysia. General: Broadly distributed in the Indian Ocean from the Persian Gulf to the Bay of Bengal; Indo-West Pacific known from the Gulf of Thailand, Indonesia, Borneo, and the Philippines.

Remarks *Carangoides praeustus* is reported to occur in Malaysia waters except west coast of East Malaysia (Smith-Vaniz 1999). However, this species has been reliably reported from Sarawak water (Annie and Albert 2009). Present study showed this species is easily found in Sulu Sea and Celebes Sea. On the contrary, we have no confirmed records of any occurrence from Peninsular Malaysia waters.

Fig. 14 *Carangoides praeustus,* UMTF9526, 12.5 cm SL

Carangoides talamparoides Bleeker 1852
(English name: Imposter Trevally)
(Local name: Demuduk Rambai)
(Fig. 15; Table 2)

Carangoides talamparoides Bleeker 1852: 91 (type locality: Indonesia, western Sumatra, Sibogha; lectotype: RMNH 6099).

Carangoides talamparoides – Mansor et al. 1998: 145; Ambak et al. 2010: 123; Atan et al. 2010: 39a (Sabah); Ahmad et al. 2018: 83.

Material examined CT01–CT07, SB21, SB58, SB43, SB72, SB146, SB147, SB149, SB169, SB171.

Diagnosis Dorsal-fin rays VIII + I, 21–23 (mainly 22); anal-fin rays II + I, 17–19 (18). Lateral-line scales 65–82; lateral-line scutes 21–31; total elements on straight part of lateral line 30–37. Gill rakers 7–9 (8) + 21–23 (21) = 28–32 (29). Body oval and strongly compressed. Dorsal profile of snout steep and nearly straight to above eye. Snout blunt. Breast naked ventrally to distinctly behind origin of pelvic fin, often extending to anal spine; laterally, naked area of breast extends to naked based of pectoral fin, including small area present just above pectoral fin base. No filamentous rays on dorsal and anal fins. Curved part of lateral line longer than straight part. Caudal fin central rays dusky yellow with black distal margin.

Coloration Body silvery blue dorsally and silvery white on sides and ventrally. A small black spot on operculum. Tongue white to pale grey. Soft dorsal and anal fins white to dusky with white spots bordered by faint yellow margins on membranes between rays of anal fin.

Size Largest specimen examined 216 mm fork length. The maximum recorded size by FAO for this species is 280 mm fork length.

Distribution Malaysia: Widespread in Peninsular Malaysia, Sabah and Sarawak. General: Widespread in Indo-west Pacific Ocean from Gulf of Thailand, Sumatra, Borneo, Philippines, Guam and Australia. In the western Indian ocean distributed from the Gulf of Oman eastward to Sri Lanka. This species also occurs in the Red Sea.

Fig. 15 *Carangoides talamparoides,* UMTF9527, 12.7 cm SL

Table 3 Inter- and intra-specific genetic distances for 13 species of Malaysian *Carangoides*

		1. CA	2. CB	3. CC1	4. CC2	5. CC3	6. CCR	7. CD	8. CF	9. CFV	10. CG1	11. CG2	12. CH	13. CM	14. CO	15. CP	16. CT
1	*C. armatus*	**0.003**															
2	*C. bajad*	0.149	**0.001**														
3	*C. coeruleopinnatus* 1	0.121	0.145	**0.013**													
4	*C. coeruleoponnatus* 2	0.121	0.152	0.032*	**N/A**												
5	*C. coeruleopinnatus* 3	0.120	0.138	0.089*	0.071*	**N/A**											
6	*C. chrysophrys*	0.146	0.150	0.137	0.136	0.140	**0.003**										
7	*C. dinema*	0.134	0.154	0.133	0.128	0.116	0.151	**0.001**									
8	*C. ferdau*	0.158	0.164	0.149	0.153	0.154	0.149	0.115	**0.001**								
9	*C. fulvoguttatus*	0.103	0.150	0.101	0.098	0.091	0.133	0.127	0.131	**0.001**							
10	*C. gymnostethus* 1	0.103	0.142	0.089	0.090	0.083	0.149	0.126	0.145	0.045	**0.005**						
11	*C. gymnostethus* 2	0.120	0.145	0.108	0.112	0.096	0.155	0.133	0.147	0.056	0.030*	**N/A**					
12	*C. hedlandensis*	0.114	0.165	0.127	0.127	0.125	0.162	0.145	0.156	0.126	0.125	0.144	**0.006**				
13	*C. malabaricus*	0.140	0.137	0.130	0.119	0.136	0.073	0.148	0.132	0.119	0.133	0.140	0.152	**0.008**			
14	*C. oblongus*	0.138	0.160	0.128	0.128	0.134	0.154	0.066	0.107	0.137	0.131	0.132	0.149	0.147	**0**		
15	*C. preaustus*	0.188	0.193	0.191	0.181	0.190	0.204	0.167	0.183	0.191	0.188	0.180	0.178	0.173	0.171	**0**	
16	*C. talamparoides*	0.134	0.136	0.131	0.117	0.130	0.070	0.139	0.132	0.109	0.130	0.134	0.151	0.024	0.153	0.179	**0.007**

Value in bold represents mean intra-specific genetic distance values, *Atypical intra-specific genetic distance, *N/A* Not available

Remarks See *C. coeruleopinnatus* and *C. malabaricus* for comparison with *C. talamparoides*. Present study provides the first specimen-based records of its occurences in Malaysia waters. This species is common and widely distributed in Malaysia waters. Present study provides the additional known distribution to west coast of East Malaysia and its occurences extending to Celebes Sea.

COI Divergence Among Malaysian *Carangoides*

A total of 144 sequences were assessed for COI divergence. The number of sequences per species collected varied between three (*C. bajad* and *C. praeustus*) to 35 (*C. coeruleopinnatus*). An additional 124 COI sequences of *Carangoides* from BOLD Systems (Project code: DBMF) were also included to support the current analyses and verify earlier analysis (Mat Jaafar et al. 2012). Therefore, the final data set consisted of 268 COI sequences of genus *Carangoides* from Malaysian waters (Table 1). No insertions/deletions, heterozygous sites or stop codons were observed, supporting the view that all the amplified sequences constitute functional mitochondrial COI sequences.

The average within species K2P distance was 0.4%, with *C. oblongus* and *C. praeustus* showing the lowest mean intraspecific divergence (0%) and *C. coeruleopinnatus* having the highest (1.3%). *Carangoides coeruleopinnatus* and *C. gymnostethus* showed deep intraspecific divergence with maximum nucleotide divergence of 8.9% and 3.0% respectively (Table 3). All the sequences clustered into 94 putative haplotypes (ESM1) in the ML tree with each clustering in its own putative taxon (Fig. 16) with high bootstrap support (> 96%) except for *C. coeruleopinnatus* (56%) and *C.*

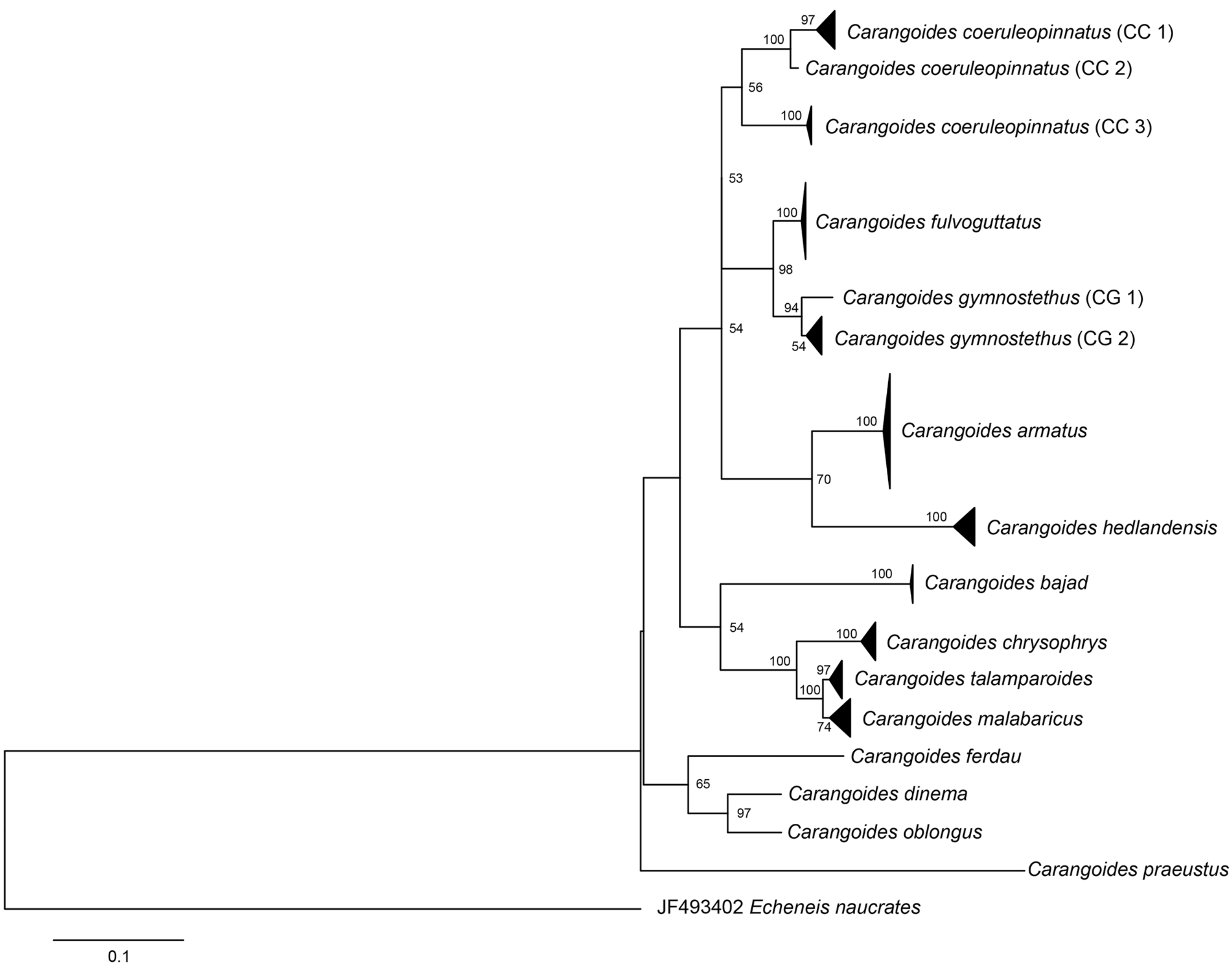

Fig. 16 Maximum-likelihood tree of COI for all *Carangoides* species collected from Malaysia. Tips represent collapsed haplotype sequences for all individuals within the same species, except for *C. coeruleopinnatus* (CC1, CC2 and CC3) and *C. gymnostethus* (CG1 and CG2), where three and two groups were retained to show the presence of separate highly supported divergent lineages, see Table 3 and ESM1. All bootstrap values for conspecific groups were > 50%

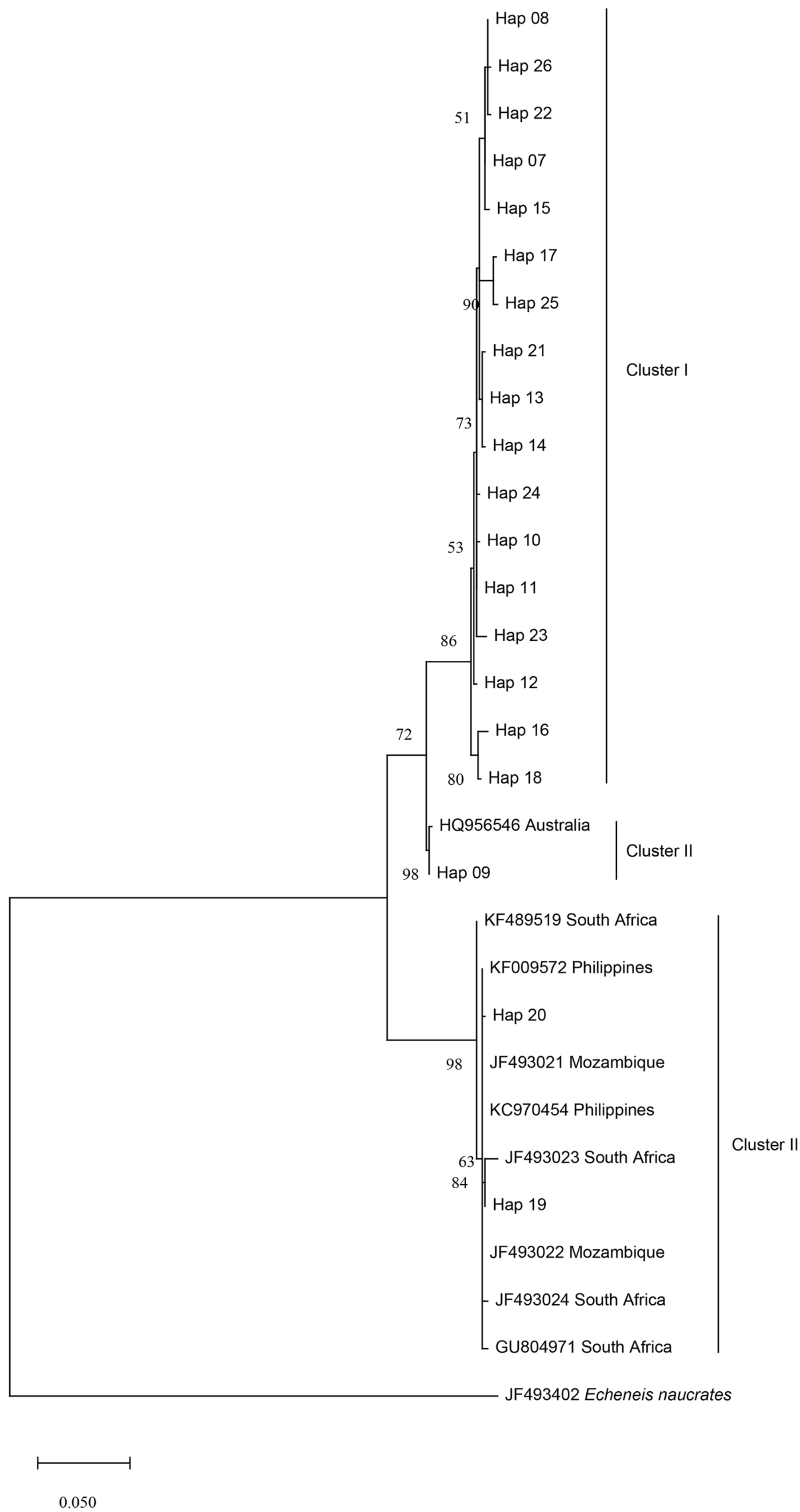

Fig. 17 Maximum-likelihood tree of *C. coeruleopinnatus* COI haplotypes with additional sequences from GenBank for comparison

gymnostethus (94%). These two species (*C. coeruleopinnatus* and *C. gymnostethus*) which showed deep intraspecific divergence formed three and two clusters within their own group, respectively (Figs. 17 and 18). Although divergent, specimens of these separate clusters were more similar to each other than to specimens of any other species in our data set. ABGD results based on K2P distance delineated 16 clusters, which was concordant with ML analysis.

Deep Intraspecific Divergence

The 74 specimens of *C. coeruleopinnatus* were divided into three clusters in the ML tree (Fig. 17). Cluster I comprised of the majority of the specimens from all localities in Malaysia with 86% bootstrap value. Cluster II consisted of only a single specimen from Pekan, Pahang (Hap 09), while three specimens from Kudat (Hap 19) grouped in Cluster III.

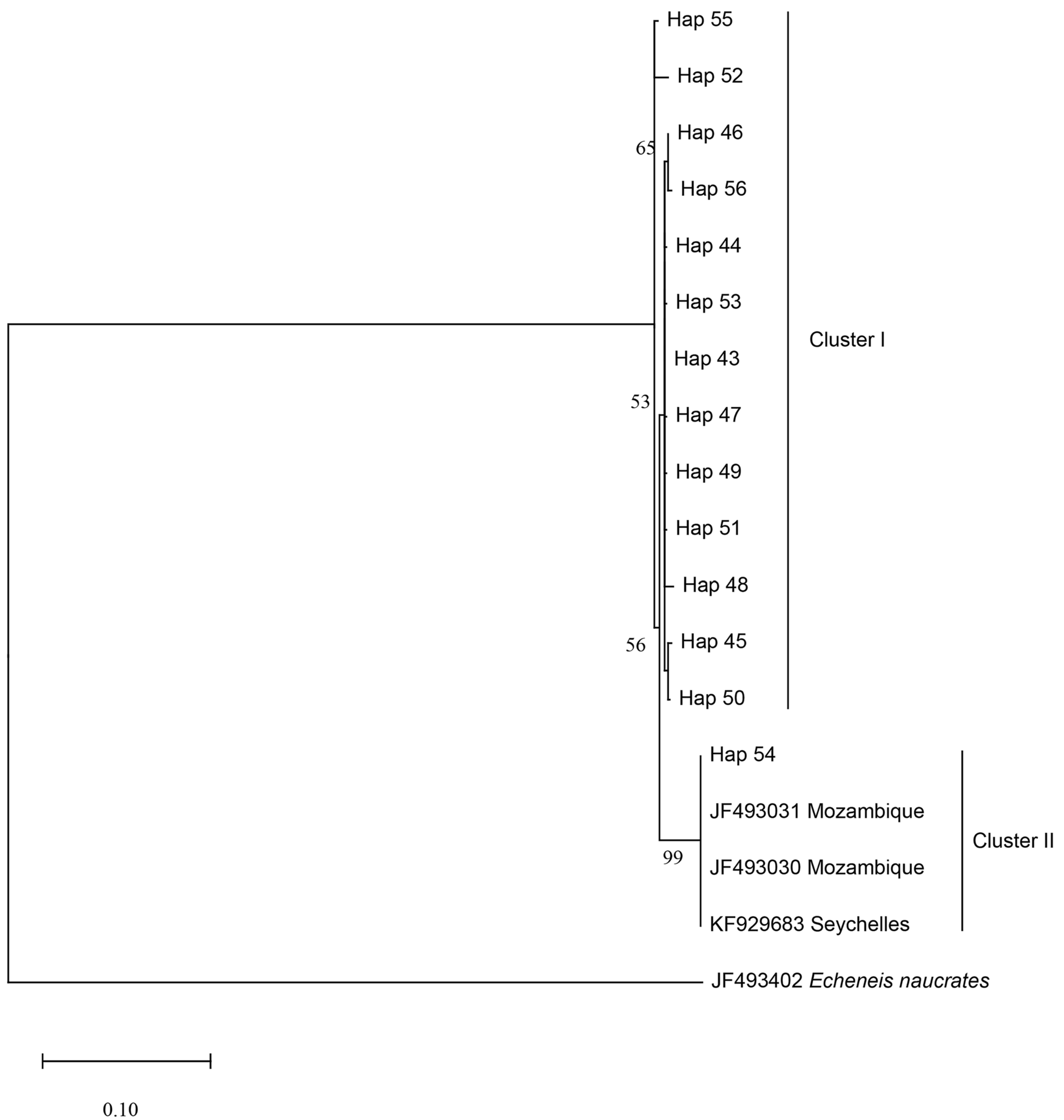

Fig. 18 Maximum-likelihood of *C. gymnostethus* COI haplotypes with additional sequences from GenBank for comparison

BLAST searches of Cluster II individual revealed a 99.8% sequence similarity to *C. coeruleopinnatus* voucher specimen from Australia (HQ956546). In Cluster III, BLAST searches revealed 99% sequence similarity to *C. coeruleopinnatus* voucher specimen from the Philippines (KC970454, KF009572), Mozambique (JF493021, JF493022) and South Africa (KF489519, GU804971, JF493023, JF493024). The average sequence divergence between Cluster I and II, Cluster I and III and Cluster II and III were 3.2%, 8.9% and 7.1%, respectively (Table 3).

Carangoides gymnostethus also showed deep intraspecific divergence among the 38 specimens (maximum of 3.0% pairwise nucleotide divergence) and formed two clusters in the ML tree (Fig. 18). Cluster I was the major cluster comprised of specimens from all localities from Malaysia, while Cluster II consisted of only a single specimen from Bagan Panchor, Perak (Hap 54). BLAST search of Cluster II however, showed 100% sequence similarity to *C. gymnostethus* from Mozambique (JF493031, JF493030) and Seychelles (KF929683). The average sequence divergence between Cluster I and II was 3.0%. These deep intraspecific divergences provide strong evidence of at least three and two lineages of *C. coeruleopinnatus* and *C. gymnostethus* respectively, in Malaysian waters.

Public Databases Sequences Analysis

To assess the accuracy of species identification of voucher sequences in public databases such as the GenBank, we conducted a phylogenetic analysis of additional 108 COI sequences of all *Carangoides* species from other regions. The constructed ML tree (not shown) revealed that 25 sequences did not cluster in their own taxa (Table 4). These findings highlight the taxonomic confusion between a few species within the genus *Carangoides*.

Discussions

First Specimen-Based Records of Malaysian *Carangoides*

Our survey on *Carangoides* species in Malaysian waters was conducted from 2016 to 2017. Our extensive survey of the surrounding seas of Malaysia successfully sampled 13 of the 16 *Carangoides* species documented in this region by FishBase. We failed to obtain *C. equula*, *C. orthogrammus* and *C. plagiotaenia* even though their occurrences have been reported in neighbouring areas by

Table 4 Probable misidentification of 25 GenBank sequences which did not group in its presumed taxon in the current NJ tree

GenBank accession number	GenBank sequence assignment	Current NJ tree assignment
KF714904 (unpublished)	*C. malabaricus*	*C. coeruleopinnatus*
KF809393 (unpublished)	*C. malabaricus*	*C. coeruleopinnatus*
KF009570 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
EF607338 (Zhang 2011)	*C. chrysophrys*	*C. coeruleopinnatus*
EF607339 (Zhang 2011)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237670 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237671 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237673 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
KF009571 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237672 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237669 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
FJ237668 (unpublished)	*C. chrysophrys*	*C. coeruleopinnatus*
MF375310 (Bogorodsky et al. 2017)	*C. talamparoides*	*C. coeruleopinnatus*
MF375313 (Bogorodsky et al. 2017)	*C. talamparoides*	*C. coeruleopinnatus*
MF375315 (Bogorodsky et al. 2017)	*C. talamparoides*	*C. coeruleopinnatus*
KP856782 (unpublished)	*C. bajad*	*C. gymnostethus*
KC508507 (unpublished)	*C. talamparoides*	*C. chrysophrys*
FJ347880 (Lakra et al. 2011)	*C. malabaricus*	*C. chrysophrys*
FJ347881 (Lakra et al. 2011)	*C. malabaricus*	*C. chrysophrys*
FJ347879 (Lakra et al. 2011)	*C. malabaricus*	*C. chrysophrys*
FJ347878 (Lakra et al. 2011)	*C. malabaricus*	*C. chrysophrys*
FJ347935 (Lakra et al. 2011)	*C. malabaricus*	*C. chrysophrys*
KX512695 (Damerau et al. 2018)	*C. malabaricus*	*C. talamparoides*
HQ149818 (Asgharian et al. 2011)	*C. malabaricus*	*C. talamparoides*
KP856785 (unpublished)	*C. chrysophrys*	*C. talamparoides*

Global Biodiversity Information Facility (GBIF.org). The abundance and composition of species varied from different areas around the coastlines of Malaysia and from different marine regions. The most abundant species that were common in almost all areas in Malaysia were *C. armatus*, *C. chrysophrys*, *C. coeruleopinnatus*, *C. gymnostethus*, *C. hedlandensis* and *C. malabaricus* (Table 1). *Carangoides praeustus* is restricted to the Sulu and Celebes Seas as we only collected specimens from Tawau and Beluran, Sabah. Additionally, we also collected the first specimen-based records of *C. oblongus* and *C. talamparoides* in Malaysia. *Carangoides oblongus* is known to be widely spread in Malaysian waters (Smith-Vaniz 1999). However, it is common in Sabah but rarely found in Sarawak and Peninsular Malaysia. There was only one photographic record found from Sarawak by Annie and Albert (2009). Our survey managed to collect a single specimen of *C. oblongus* from Bagan Panchor, Perak (UMTF9523). This finding confirmed the range extension of *C. oblongus* were from East Malaysia (Sabah) to west coast of Peninsular Malaysia. However, we have yet to find any occurrence from the east coast of Peninsular Malaysia. Previously, *C. talamparoides* has been recorded in Malaysia through several local fish identification books that provide evidence of the existence of the species in Malaysia, however none of them could confirm the exact location their specimens been collected and preserved (Mansor et al. 1998; Ambak et al. 2010; Ahmad et al. 2018). Only Atan et al. (2010) confirmed the presence of *C. talamparoides* in Sabah through photo evident. Our sampling survey manage to confirm the species is common and widely distributed from west coast of Peninsular Malaysia until Celebes Sea.

Based on the Annual Fisheries Statistics of the Department of Fisheries Malaysia (DOF), *Carangoides* landings are consistent throughout the year and there is no seasonal variation in *Carangoides* catches. Thus, failure to collect the remaining three species (*C. equula*, *C. orthogrammus* and *C. plagiotaenia)* is unlikely to be influenced by seasonality of sampling. A quick search in GBIF.org confirmed that these three species have never been recorded by local taxonomists. The occurrences of *C. orthogrammus* in Malaysia were reported based on observations during scuba diving activities near Tenggol Island, Terengganu, October 2015, in an online citizen science database (Diveboard; https://www.diveboard.com) linked to GBIF.org (2019). In the case of *C. equula*, four occurrences were recorded in South China Sea near the Sarawak coastlines in 2014 and 2015. However, the specimens are kept by the European Nucleotide Archive (2019). *Carangoides equula* specimens are also deposited at the Natural History Museum London (Natural History Museum 2014) but the exact sampling location is not available. Three occurrences of *C. plagiotaenia* in Malaysian waters have been recorded. One occurrence was observed in 1994 by divers (National Museum of Nature and Science Japan 2019) and the other two were recorded as preserved specimens collected in 1909 by the National Museum of Natural History, Smithsonian (Orrell 2019). However, there is no record of the coordinates of the collection sites. From the perspectives of previous Malaysian literature records of the three species, we only have photo evidence without museum specimens and sampling localities to confirm these records. In order to facilitate identification of these species, we included them to the identification key to Malaysia species of *Carangoides*.

Ambiguous Usage of Local Names in Malaysia

The annual landings of many closely related fish species in Malaysia are currently reported as a single collective group, rather than as an individual species. In fisheries management, fishery managers should take into consideration the different biological parameters of fish species, where different species may have different biological characteristics such as age, growth, reproduction, recruitment, or mortality. This will influence the threat to their population sustainability, where most vulnerable species will be threatened more compared to the least vulnerable species. Thus, Mat Piah et al. (2018) calls for better data collection by the DOF where the data should be presented at the species level, rather than as a single collective group so that the real exploitation of fisheries resources can be well understood. Current marine fish landing statistics by DOF (2018), pool the *Carangoides* species under two main groups according to the local name; 1. “Cermin/Sagai/Cupak” and 2. “Demuduk”. However, there is no detailed explanation on how these 13 species are categorized into this local name groups. According to Ahmad et al. (2018) and Atan et al. (2010), in general the valid local name of all *Carangoides* in Malaysia is “Demuduk”, while “Cermin” refers to the cleftbelly trevally, *Atropus atropos*, which is morphologically similar to genus *Carangoides*. However, in some instances or localities the “Demuduk” is interchangeably used Cermin, Cupak, Putih, Rambai and Sagai. This ambiguous usage of valid local names of marine species is a major concern in Malaysian fisheries. The inconsistency of local names used in the DOF statistics report and fish identification books by local taxonomists (Mohsin and Ambak 1996; Annie and Albert 2009; Ambak et al. 2010; Atan et al. 2010; Ahmad et al. 2018) leads to confusion in determining the precise landings of individual species. Thus, landing statistics do not reflect the precise number of individual species harvested and the true status of species exploitation pattern which will hinder efficient sustainable exploitation of a particular species.

Establishment of a Reliable *Carangoides* DNA Library

Taxonomic ambiguities in the genus *Carangoides* due to morphological and meristic similarities across species, as well as plasticity in body shape, size, and color patterns (Froese and Pauly 2019) have been well noted and frequently lead to misidentification among *Carangoides* species. This is further compounded by the significant changes in morphology and pigmentation during growth, observed in this genus as reflected by the numerous species synonyms in FishBase citations. Using the DNA barcoding approach, we have successfully discriminated all *Carangoides* specimens into 13 distinct species. Furthermore, three additional sub-clusters were observed within two species due to deep intraspecific divergence.

The accuracy of species identification through DNA barcoding approach depends on the availability of an exact or near match DNA sequence of the species in the database. Unknown specimens can only be compared if the species has been previously recorded in the database. The international campaign, FISH-BOL encourages researchers to deposit their fish sequences to GenBank and BOLD System which can be used by non-taxonomists to identify unknown specimens. However, to deposit data in these public databases, one needs to ensure correct scientific naming and provide high-quality COI sequences to avoid ambiguous results. Seah et al. (2017) recorded 34% misidentification in the COI GenBank sequences of the family Leiognathidae. Overlapping morphological characters among closely related species is the most likely factor for the observation. Indeed, taxonomic uncertainties have been well reported among species within family Leiognathidae (Puckridge et al. 2013). However, the former also noted that 6% of the misidentified sequences were also connected to ambiguous sites due to low quality sequences. Therefore, it is important to deposit accurate data as only then can they be of significant contribution to the global DNA barcoding effort to document and catalogue the diversity of life. The current study has successfully developed a DNA barcode library for *Carangoides* fishes in Malaysia as a reliable reference for identification of genus *Carangoides* worldwide.

Cryptic Lineages in the *Carangoides* spp. Complex

DNA barcoding has been extensively used as a species identification tool for a wide range of fish species (Zhang and Hanner 2011; Ward et al. 2005; Mat Jaafar et al. 2012; Chang et al. 2017; Bakar et al. 2018; Fadli et al. 2020). However, in the process of building up a reference library, deep genetic divergences within nominal species are commonly found, as observed in the current study. The current study delineated two *Carangoides* species, *C. coeruleopinnatus* and *C. gymnostethus* into three and two discrete lineages, respectively with range pairwise nucleotide divergence of 3.0% to 8.9% which still lies within the limit of the 2% intra-specific variation as proposed by Ward (2009). Mean levels of COI divergence range in other fish groups were recorded between 0.2 –0.4% with genetic distance values ranging from 0–25.0% in family Carangidae (Mat Jaafar et al. 2012), 0–22.0% in Family Platycephalidae (Puckridge et al. 2013), 0–20.5% in genus *Lutjanus* (Bakar et al. 2018) and 0 –21.8% in genus *Nemipterus* (Imtiaz et al. 2016). However, the observed inter-subcluster genetic distances were atypical of population level diversity; *C. coeruleopinnatus* (3.2%–8.9%) and *C. gymnostethus* (3.0%) and no geographic structuring was detected (subcluster II grouped with Australia; subcluster III grouped with South Africa, the Philippines, and Mozambique for *C. coeruleopinnatus*; subcluster II grouped with Mozambique and Seychelles for *C. gymnostethus*). Divergent as they were, all individuals were grouped in their respective taxa in the phylogenetic tree.

Deep divergences within species are commonly attributed to specimen misidentification (Seah et al. 2017). However, marked discordance between molecular and morphological diagnoses are now also frequently acknowledged as an emergence of cryptic or unrecognized speciation events, which a new divergent clade will be apparent that is different from that of any currently recognized species (Mat Jaafar et al. 2012, 2020b; Lim et al. 2016; Milá et al. 2017; Bakar et al. 2018; Kakioka et al. 2018). Hebert et al. (2004) proposed the '10 × rule' as indicator of cryptic speciation where individuals are flagged as possible cryptic species if they diverge by 10 times or more than the average of typical intraspecific variability of the group. Another approach proposed by Ward et al. (2009) showed that individuals which diverged by or more than 3% nucleotide divergence within the same species were more likely to be congeneric than conspecific. In the case of *C. coeruleopinnatus*, all clades were in agreement with Hebert '10 × rule' and Ward's 3% nucleotide divergence, Clade I vs Clade II was 3.2%, Clade I vs Clade III was 8.9% and Clade II vs Clade III was 7.1%. In the case of *C. gymnostethus*, Clade I vs Clade II diverge by 3.0% for species assignment.

Cryptic diversity has been identified within species, especially when it is used in conjunction with morphological and ecological methods. Several examples of deep COI divergence within marine fish species have been attributed to cryptic speciation (Mat Jaafar et al. 2012, 2020a, b; Martinez-Takeshita et al. 2015; Lim et al. 2016; Bakar et al. 2018). The high levels of intraspecific divergence highlight the utility of DNA barcoding in not only enabling species identification and delimitation, but also flagging the existence of putative new taxa. The discovery of more than two lineages of marine fishes has proofed that DNA barcoding has been particularly helpful in assessing marine biodiversity.

Probable Misidentification of GenBank Specimens

Detailed inspection of GenBank *Carangoides* species sequences and comparison with the present *Carangoides* specimens found numerous discrepancies between both datasets. These mainly involved *C. malabaricus*, *C. chrysophrys*, *C. talamparoides* and *C. coeruleopinnatus*. *Carangoides malabaricus*, *C. talamparoides* and *C. coeruleopinnatus* are very similar to each other in general body shape and coloration and had previously been grouped within the *Malabaricus* group (Williams and Venkataramani 1978) which showed almost similar external morphology. Generally, *C. malabaricus* and *C. talamparoides* can be distinguished from other species of *Carangoides* including *C. chrysophrys* and *C. coeruleopinnatus* on the basis of breast squamation. They are the only species in which the naked area on the breast extends above the pectoral fin base, compared to *C. chrysophrys* and *C. coeruleopinnatus* which has a scaly area above the pectoral fin base. However, such character can only be discerned through proper inspection. On the other hand, *C. malabaricus*, *C. talamparoides* and *C. coeruleopinnatus* can be differentiated from each other by the total number of gill rakers. *Carangoides malabaricus* has the highest count of gill rakers with 31–37, followed by *C. talamparoides* (28–32) and *C. coeruleopinnatus* (21–25). Furthermore, there is a degree of overlapping in counts between *C. coeruleopinnatus* and *C. talamparoides* recorded by Gunn (1990) (23–27 and 26–30, respectively) and Bogorodsky et al. (2017) (21–27 and 25–31, respectively). Bogorodsky et al. (2017) also recorded overlapping between *C. talamparoides* (25–31) and *C. malabaricus* (32–38). With the case of overlapping gill rakers, another character can be used as suggested by Gunn (1990) which was tongue color and dentition (see remarks of *C. coeruleopinnatus*).

Carangoides chrysophrys can be distinguished from other species of *Carangoides* by having the snout abruptly vertical above the mouth cleft in adults. These three species together with *C. chrysophrys* are often collectively sold as a group in the local market. *Carangoides talamparoides* has been recorded in the Red Sea (Bogorodsky et al. 2017) although its eastern limit was reported to be in the Oman Sea. However, total gill rakers of the seven specimens examined was 23–26 which would classify it as *C. coerulopinnatus*. A reanalysis of several sequences of Red Sea origin (MF375310, MF375313 and MF375315) with the current study clustered them with *C. coeruleopinnatus* instead of *C. talamparoides*.

Ambiguity between *C. bajad* and *C. gymnostethus* (Table 4) was also observed among the GenBank specimens. However, through our detail inspection of our specimens for both species, C. *bajad* can be easily distinguished from the other species of *Carangoides* by having completely scaly breast and sides of body covered by numerous yellow spots. Compared to *C. bajad*, breast of *C. gymnostethus* is naked ventrally beyond insertion of pelvic fin and laterally naked to pectoral fin base. On the other hand, *C. gymnostethus* is much more similar to *C. fulvoguttatus* in general body shape and coloration but can be clearly distinguished from *C. gymnostethus* by the location of the mouth cleft. The mouth cleft is located below the lower margin of the eye in *C. fulvoguttatus* while in *C. gymnostethus* the mouth cleft is located at the same level as the lower margin of the eye. Other characters separating the species are gill rakers and soft dorsal-fin rays count. In *C. fulvoguttatus*, total gill rakers 24–27 and soft dorsal-fin rays 26–28; in *C. gymnostethus*, total gill rakers 28–30 and soft dorsal-fin rays 29–31.

As a conclusion, fish diversity in Malaysia is highly threatened by overexploitation and anthropogenic pressure. With the significant decline in biodiversity, species extinction enhances the need for the conservation of marine biodiversity. Our results reveal that DNA barcoding was successful in discriminating congeneric species within family Carangidae. Identification through morphological examination supported by DNA barcoding could be used to evaluate fish biodiversity, monitor fish conservation, and manage fisheries resources. Barcodes data provided in current study will provide direction for future studies of fish species that need to be barcoded. Once a fish DNA barcode database has been established, the scientific and practical benefits of fish barcoding are diverse. The result will facilitate fisheries managers, ecologist, and policy makers to develop policies for the conservation and sustainable use of fisheries resources.

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Author Contribution Tun Nurul Aimi Mat Jaafar and Ying Giat Seah contributed to the study conception and coordinated the research. Material preparation, data collection and analysis were performed by Salwani Abdullah and Nuralif Fakhrullah Mohd Nur. The first draft of the manuscript was written by Nuralif Fakhrullah Mohd Nur. Siti Azizah Mohd Nor, Min Pau Tan, Rumeaida Mat Piah and Ahasan Habib assisted in analysis and interpretation of data. All authors have critically gone through the manuscript and provided suggestions. All authors reviewed, finalized and approved the manuscript.

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Availability of Data All data generated during this study are included in this article. Information regarding sequences of the present study has been deposited in NCBI, GenBank (www.ncbi.nlm.nih.gov) under accession numbers MT646199–MT646345.

Code Availability Not applicable.

Declarations

Ethics Approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated vertebrate species. These species are not in the IUCN list of endangered or protected species. Only dead specimens were sampled from the local wet markets.

Competing Interests The authors declare they have no competing interests.

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