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Review of the Mackerel Genus *Rastrelliger* (Teleostei: Scombridae) with Redescription of *R. chrysozonus* (Rüppell, 1836) and *R. kanagurta* (Cuvier, 1816) †

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Abstract: The Indo-West Pacific scombrid genus *Rastrelliger* Jordan & Starks is reviewed. Formerly, the genus was considered to contain three valid species, viz., R. *brachysoma* (Bleeker, 1851) known from the south-east coast of India to Samoa Islands; R. *faughni* Matsui, 1967 reported from the south-east coast of India to Fiji; and R. *kanagurta* (Cuvier, 1816), the most widespread species known from the east coast of Africa and the Persian/Arabian Gulf east to Tonga. Herein, R. chrysozonus (Rüppell, 1836), restricted to the Red Sea, is resurrected from the synonymy with *R. kanagurta* and both species are redescribed in detail, based on an integrative morphological and molecular assessment. Consequently, *Scomber microlepidotus* Rüppell, 1836 is moved from the synonymy with *R. kanagurta* to synonymy with *R. chrysozonus*. *Rastrellidger chrysozonus* differs from *R. kanagurta* primarily by a longer upper jaw. *Rastrelliger brachysoma* differs from the other three species by a deeper body, a deeper caudal peduncle, and a very long intestine. *Rastrelliger faughni* differs from the other three species in having a more slender body, usually X spines in the first dorsal fin (versus IX spines), shorter and fewer gill rakers, a shorter maxilla, and a shorter intestine. The phylogenetic analysis of mitochondrial genes of all Rastrelliger species also demonstrated that R. chrysozonus forms a well divergent evolutionary lineage, with *R. kanagurta* being its closest relative. In addition to the redescriptions of *R. chrysozonus* and *R. kanagurta*, brief species accounts for *R. brachysoma* and *R. faughni* and the key to the four species are provided.

Keywords: Scombroidei; *Scomber*; Indo-West Pacific; phylogenetic analysis; integrative taxonomy

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1. Introduction

The scombrid genus *Rastrelliger* Jordan and Starks, 1908 (Scombridae) is a group of semi-pelagic fishes of the tribe Scombrini, confined to tropical and subtropical coastal waters of the Indo-West Pacific. They often form large feeding aggregations, filtering zooplankton with long gill rakers while keeping their mouth open. Although they are medium-sized fishes that rarely exceed 30 cm in fork length, they are commercially important in some South Asian countries [1–3].

The first described species of the genus is *Scomber kanagurta*, a description of which is attributed to Cuvier (1816) [4], based on Russell's (1803) [5] figure and description of a specimen taken from Indian waters. Rüppell (1828) [6] was the first to mention *S. kanagurta* from the Red Sea, subsequently describing two Red Sea species: *Scomber chrysozonus* Rüppell, 1836 and *Scomber microlepidotus* Rüppell, 1836. Later, Klunzinger (1871) [7] provided a brief species account of *S. kanagurta*, placing *S. chrysozonus* in its synonymy, but listed *S. microlepidotus* as a valid species without justification.

The genus *Rastrelliger* was established by Jordan and Starks in Jordan and Dickerson (1908) [8] for species with very long gill rakers, contrasting the moderately short gill rakers in *Scomber* Linnaeus, 1758, with the type species *Scomber brachysoma* Bleeker, 1851 from Indonesian waters. They also placed *S. kanagurta* (with authors as Cuvier and Valenciennes, 1832), *Scomber loo* Lesson, 1829 (with authors as Cuvier and Valenciennes, 1832), and *S. microlepidotus* within the genus but without detailing features for distinguishing these species. These authors, however, provided details on osteological characters that allowed distinction between *Rastrelliger* and *Scomber*. Later, some authors (e.g., Herre 1941 [9]) continued using the name *S. microlepidotus* as a valid species without any comments, whilst Jones et al. (1961) [10] considered *S. microlepidotus* to be a junior synonym of *R. kanagurta*, but also provided no clarification of his reasoning.

In their preliminary review of the family Scombridae, Collette and Gibbs (1963) [11] recognized two species in *Rastrelliger* as valid, viz., *R. brachysoma* and *R. kanagurta*, synonymizing *R. chrysozonus* with the latter. Matsui (1967) [12] provided extensive comparative analysis between *Scomber* and *Rastrelliger* and recognized three valid species in the latter genus: *R. brachysoma*, *R. kanagurta*, and his new species, *R. faughni*. More recently, Collette and Nauen (1983) [2], Collette (2001) [1], and Collette and Graves (2019) [3] published comprehensive data on all three species of *Rastrelliger*, listing the two nominal species from the Red Sea, *R. chrysozonus* and *R. microlepidotus*, as synonyms of *R. kanagurta*. In more recently published checklists of Red Sea fishes (e.g., [13,14]), *R. kanagurta* was listed but without comments on its Red Sea synonyms. Thus, by the beginning of the present study, three nominal species were recognized as valid in the genus *Rastrelliger*.

As part of recent biodiversity surveys, jointly conducted by King Abdulaziz University and Senckenberg Research Institute and Natural History Museum Frankfurt along the Saudi Arabian coast of the Red Sea, numerous specimens identified as *R. kanagurta* were trawled off Jizan, southern Saudi Arabia [15]. A close comparison of these specimens with *R. kanagurta* from other areas of the Indo-West Pacific revealed that these Red Sea specimens are morphologically and genetically distinct and represent a separate species. Examination of Rüppell's types confirmed that *R. chrysozonus* is the valid name for the Red Sea specimens; consequently, *R. microlepidotus* becomes a junior synonym of the former.

This study reviews the genus *Rastrelliger*, redescribing *R. chrysozonus* and *R. kanagurta*, providing diagnostic characters for these two species and comparisons with related species (*R. brachysoma* and *R. faughni*), and clarifying the taxonomic status of other nominal species. Phylogenetic analyses of available mitochondrial cytochrome c oxidase subunit I (COI), cytochrome b (*cyt b*), and 16S ribosomal DNA (16S rDNA) sequence data showed that the four species represent divergent lineages. We also provide COI barcodes of the morphologically examined specimens of *R. chrysozonus* for future means of identification by molecular barcoding.

2. Materials and Methods

2.1. Materials

We examined the morphology of 60, 60, 24, and 73 non-type specimens of *R. brachysoma*, *R. chrysozonus*, *R. faughni*, and *R. kanagurta*, respectively. We also examined the type specimens of eight nominal species. For the molecular phylogenetic analysis, we newly determined the COI and *cyt b* sequences of seven and one non-type specimens of *R. chrysozonus* and *R. kanagurta*, respectively. These were supplemented by the sequences retrieved from GenBank and Barcode of Life Data Systems (BOLD Systems: http://www.boldsystems.org (accessed on 5 December 2024), which included the sequences of the other two species and another locus (16S rDNA). More details are provided in Supplementary Table S1 (Table S1) and the "Material examined" section in each species' account.

2.2. Morphological Analysis

Measurements and counts followed earlier studies [16,17], except for the following which followed a more recent work [18]: upper-jaw length (lacrimal length) was measured from the tip of the snout to the posterior end of the lacrimal; head width was taken at the posterior margin of the orbit; body width at the uppermost base of the pectoral fin; body depth 1 as the depth at the posterior margin of opercle; body depth 2 as the distance between the anterior origins of the first dorsal and pelvic fins; body depth 3 as the distance between the origins of the second dorsal and anal fins; upper peduncle length as the distance from the posterior insertion of the second dorsal fin to the posterior end of the hypural; lower peduncle length as the distance from the posterior insertion of the anal fin to the posterior end of the hypural; gill-raker length at angle as the length of the gill raker at the junction between upper and lower limbs of the first gill arch. In addition, scales between the lateral line and first dorsal fin were counted diagonally from the lateral-line scale (counted as 0.5) to the first dorsal-fin origin, excluding rudimentary scales on the dorsal-fin base. Gill rakers were counted separately on the lower and upper limbs of the first gill arch, with a raker at angle being included in the count of the lower limb. Standard length and fork length are abbreviated as SL and FL, respectively. Fork length is measured from the median anterior-most point of the head to the tip of the middle caudal-fin ray. Size is given in FL unless otherwise stated. More details are provided in Figure 1 and Supplementary Figure S1. Measurements were made point to point with a digital caliper to the nearest 0.1 mm, and then expressed as a percentage of FL and other suitable lengths. Institutional codes followed Sabaj (2016) [19], in addition to UPVMI—University of the Philippines Visayas Museum of Natural Sciences Ichthyology Collection; KAUMM—King Abdulaziz University Marine Museum, Jeddah, Saudi Arabia.

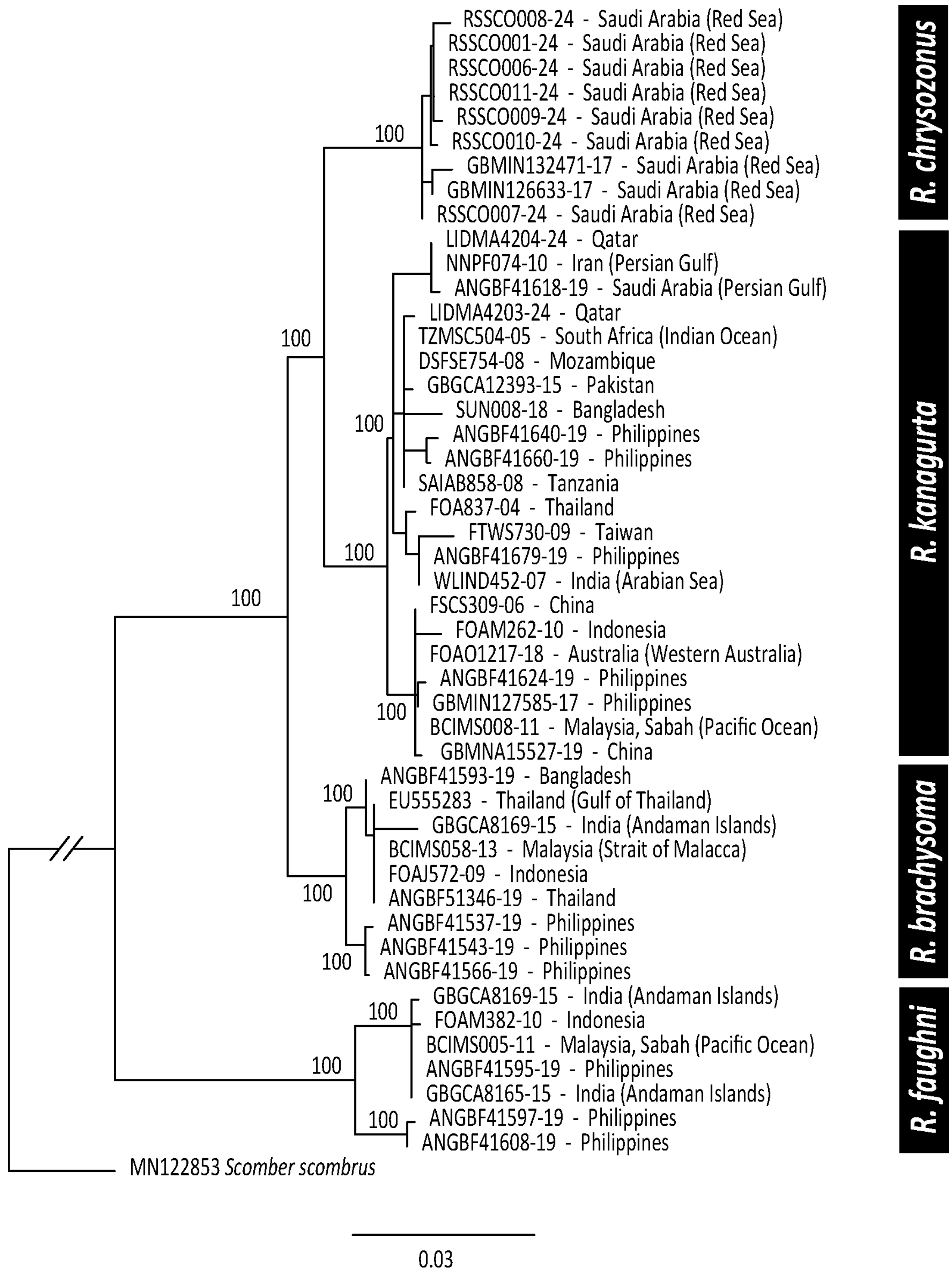

Figure 1. Maximum likelihood phylogenetic tree inferred from partial mitochondrial COI, *cyt b*, and 16S rDNA sequences (concatenated, 2383 bp in total) of four species of *Rastrelliger* with sequences of *Scomber scombrus* as outgroup. Branch length corresponds to the average rate of nucleotide substitution (see scale bar). Support values on nodes were derived from the analysis of 1000 bootstrapped datasets.

2.3. Molecular Phylogenetics

In order to investigate the evolutionary divergence of *R. chrysozonus* from the Red Sea and to assess its relationships within the genus, a maximum likelihood phylogenetic analysis was performed on partial sequences of the mitochondrial COI, *cyt b*, and 16s rDNA genes. All samples included in the analysis are listed in Table S1. Genomic DNA was isolated with a DNeasy tissue kit (Qiagen, Hilden, Germany) from 99.5% ethanol-preserved tissues of the specimens collected in this study or that had generously been provided from other collections. Amplification of the 652 bp barcoding portion of the COI gene was completed with the universal, M13-tailed primer set "COI-3" [20,21] and the PCR protocol in this study (i.e., with a constant annealing temperature of 52 °C in 35 PCR cycles) or the touchdown annealing protocol from a published work [22] (i.e., with a decreasing annealing temperature from 52 °C to 49 °C during the first 10 cycles and 25 additional cycles with a constant annealing temperature of 55 °C). In addition, partial mitochondrial *cyt b* gene sequences (1140 bp) were obtained as detailed in previous studies [18,23] using primers tailed with M13F (−21) and M13R (−27) oligonucleotides [24]. Amplicons were Sanger-sequenced from both ends with primers M13F (−21) and M13R (−27) and contigs were assembled in Geneious Pro 5.4.4 (Biomatters, Auckland, New Zealand). Alignments of COI and *cyt b* sequences obtained in this study and sequences of congeners retrieved from GenBank and BOLD were constructed with the same software. The selection of congeneric sequences was limited to a small number of specimens covering the distribution range of each species. The COI and *cyt b* alignments were concatenated with an alignment of 16S rDNA gene sequences (591 bp) of *Rastrelliger* specimens, resulting in a multiple sequence alignment of 2383 bp in length. Sequences of *Scomber scombrus* were used as an outgroup.

Prior to tree estimation, the optimal partitioning scheme and respective models of nucleotide substitution were estimated using the software PartitionFinder2 version 2.1.1 [25]: the evolution of each of the three codon positions of COI and *cyt b* genes and the 16S rDNA gene sequence were modeled using options 'rcluster' [26] and 'kmeans' [27]. The resulting optimal partition scheme suggested combining the first codon positions of the COI and *cyt b* genes (TRN + I substitution model) and the second codon positions of these genes (TRN), respectively. The third codon positions of COI (TIM + G) and *cyt b* (GTR + I + G) genes and the 16S rDNA gene (HKY) were best modelled individually. Based on the suggested partitioning scheme and models of nucleotide substitution, a maximum likelihood phylogeny was estimated with RAxML v8.2.X [28,29] using the web server-based version of the software at https://www.trex.uqam.ca (accessed on 19 August 2024) [30]. The reliability of branches in the resulting tree was inferred by 1000 replicates on bootstrapped sequence data. Estimates of inter- and intraspecific evolutionary divergence for partial COI sequences of *Rastrelliger* species were calculated in MEGA11 [31] using the Kimura 2-parameter model [32] by obtaining the number of base substitutions per site from averaging over all sequence pairs between taxa.

3. Results

3.1. Taxonomic Status of Nominal Species

An integrative morphological and molecular assessment of the types and non-types revealed that the following four species are valid: *Rastrelliger brachysoma* (Bleeker, 1851) known from the south-east coast of India to Samoa Islands; *R. chrysozonus* (Rüppell, 1836) restricted to the Red Sea; *R. faughni* Matsui, 1967 reported from the eastern coast of India to Fiji; and *R. kanagurta* (Cuvier, 1816), the most widespread species known from the east coast of Africa and the Persian/Arabian Gulf east to Tonga. *Rastrelliger chrysozonus* is herein resurrected from the synonymy with *R. kanagurta* and both species are redescribed in detail. Consequently, *Scomber microlepidotus* Rüppell, 1836 is considered to be a synonym of *R. chrysozonus*, whereas the followings are regarded as synonyms of *R. kanagurta*: *Scomber canagurta* Cuvier 1829; *Scomber loo* Lesson, 1829; *Scomber kanagurta* Cuvier in Cuvier and Valenciennes, 1832; *Scomber loo* Cuvier in Cuvier and Valenciennes, 1832; *Scomber delphinalis* Cuvier in Cuvier and Valenciennes, 1832; *Scomber moluccensis* Bleeker, 1856; *Scomber reani* Day, 1871; *Scomber lepturus* Agassiz, 1874; *Rastrelliger serventyi* Whitley, 1944. Additionally, *Scomber neglectus* van Kampen, 1907 is considered a synonym of *R. brachysoma*. More details are provided below.

3.2. Morphological and Phylogenetic Analyses

Morphological data of non-types and types are given in Tables 1 and 2, respectively. Frequency distributions of the number of gill rakers are shown in Table 3. The phylogenetic analysis of the concatenated alignment of partial sequences of two mitochondrial protein-coding genes (COI and *cyt b*) and one rRNA-coding gene (16S rDNA) resulted in a well-resolved tree, in which sequences of each of the four species of *Rastrelliger* (including *R. chrysozonus* redescribed herein) formed reciprocally monophyletic clades (Figure 1). The respective nodes were supported by high bootstrap values (100). *Rastrelliger chrysozonus* and *R. kanagurta* were the closest relatives in the resulting phylogeny. This was well corroborated by their morphological similarity (see below), which in the past led to their synonymization. Nevertheless, the closest interspecific distance was 0.03, indicative of substantial interspecific divergence (Table 4). Samples belonging to the *R. chrysozonus* clade were confined to the Red Sea, whereas samples in the *R. kanagurta* clade ranged from the Western Indian to the Western Pacific Oceans, including the Arabian Sea and the Persian/Arabian Gulf. *Rastrelliger brachysoma* was the next closely related to the species pair mentioned above, with *R. faughni* being the most divergent among the congeners (K2P distance to any of the other species >0.07). The latter two species were both represented by specimens from the Eastern Indian Ocean to the Western Pacific. All three species with Indo-Pacific distributions showed some degree of intraspecific genetic divergence, resulting in two well-supported sub-specific clades. This subdivision was most prominent in *R. faughni* with a mean inter-clade K2P distance of 0.031 (*R. brachysoma*: 0.018, *R. kanagurta*: 0.012 and *R. chrysozonus*: 0.002). Geographical distribution patterns of the two sub-clades were similar between the three species: Indian Ocean samples were confined to one of the two sub-clades, whereas Pacific samples were included in both. Note, however, that a recent search for closely related sequences of *R. faughni* via BOLD Systems showed the existence of additional, currently non-publicly available sequences of apparently intermediate divergence. Once these sequences become public for advanced phylogeographic analyses, the seemingly clear intraspecific divergence observed in the present study might be challenged. To avoid premature conclusions about the apparent phylogeographic divergence within *R. faughni* as insinuated by the phylogenetic tree shown here, we refrained from any further statistical analysis regarding the delimitation of taxonomic units in the genus *Rastrelliger*. We instead suggest performing such analyses once a more complete and geographically balanced sampling of specimens and sequences from the complete distribution range of species of the genus has been achieved.

Table 1. Proportional measurements expressed as % FL and gill-raker counts of non-type specimens of the genus *Rastrelliger*. Ranges are followed by means (for measurements) or modes (for gill-raker counts) and sample sizes in parentheses. The characters mentioned in Diagnosis, being useful in distinguishing the species, are shown in bold type. The materials examined are listed in species accounts and Table S1.

	R. chrysozonus *n* = 60	*R. kanagurta* *n* = 73	*R. brachysoma* *n* = 60	*R. faughni* *n* = 24
Fork length (FL, mm)	117.0–194.0 (60)	111.6–266.3 (73)	142.6–191.0 (60)	128.8–214.7 (24)
Measurements (in % of FL)				
Head length	**26.6–30.2 (28.5, 39)**	**26.2–29.5 (27.9, 73)**	**25.5–29.3 (27.5, 60)**	**24.4–26.5 (25.6, 24)**
Head width	—	8.1–12.1 (9.9, 73)	8.7–11.0 (9.8, 60)	8.1–10.6 (9.4, 24)
Snout length	7.6–8.8 (8.1, 17)	7.4–9.7 (8.5, 73)	7.2–8.9 (8.2, 60)	7.0–8.4 (7.6, 24)
Orbit diameter	7.2–8.0 (7.5, 14)	5.4–7.9 (6.6, 73)	5.6–8.3 (6.7, 60)	5.7–6.9 (6.4, 24)
Interorbital width	5.7–6.4 (6.1, 25)	5.4–8.6 (7.0, 73)	5.3–7.7 (6.2, 60)	5.0–8.4 (6.2, 24)
Snout to first dorsal-fin origin	35.1–37.9 (36.4, 20)	32.1–37.7 (35.0, 73)	31.7–35.8 (34.2, 60)	30.0–33.8 (32.5, 24)
Snout to second dorsal-fin origin	58.7–61.8 (60.4, 17)	56.3–61.3 (58.6, 73)	54.8–59.6 (57.0, 60)	55.2–59.6 (57.4, 24)
Snout to pectoral-finbase	**28.2–31.4 (30.1, 41)**	**26.4–30.3 (28.5, 73)**	**26.8–29.8 (28.0, 60)**	**24.7–27.5 (25.9, 24)**
Snout to pelvic-fin origin	33.1–36.5 (34.8, 41)	30.6–35.9 (33.1, 73)	30.4–36.4 (33.2, 60)	28.5–30.7 (29.7, 24)
Snout to anal-fin origin	58.5–62.7 (61.3, 17)	57.1–63.8 (60.7, 73)	55.0–62.8 (59.9, 60)	57.3–62.3 (59.6, 24)
Upper-jaw length	**15.2–16.9 (16.1, 42)**	**10.4–16.4 (14.1, 73)**	**13.2–17.8 (14.4, 60)**	**9.9–11.3 (10.7, 24)**
Body width	12.4–14.8 (13.7, 21)	10.6–14.7 (12.8, 72)	10.6–13.9 (12.3, 60)	10.8–13.1 (11.5, 24)
Body depth 1	21.0–22.9 (22.0, 22)	18.0–24.0 (20.7, 73)	22.0–25.3 (23.8, 60)	16.8–19.6 (18.4, 24)
Body depth 2	**22.4–25.1 (23.8, 38)**	**19.5–26.5 (22.8, 73)**	**24.2–28.3 (26.4, 60)**	**19.2–22.1 (20.7, 24)**
Body depth 3	20.7–24.0 (22.1, 36)	18.1–26.0 (21.5, 73)	22.9–28.2 (25.7, 60)	17.8–22.1 (19.9, 24)
Upper-peduncle length	—	23.1–28.3 (25.8, 70)	24.5–27.9 (26.1, 57)	25.4–28.8 (26.8, 23)
Lower-peduncle length	23.5–25.8 (24.5, 15)	22.9–28.1 (25.5, 73)	23.7–27.3 (25.5, 57)	24.8–27.5 (26.1, 24)
Caudal peduncle depth	**3.0–3.7 (3.4, 16)**	**3.2–4.1 (3.7, 21)**	**3.8–4.3 (4.1, 33)**	**3.3–3.8 (3.5, 12)**
Length of first dorsal-fin base	16.1–18.4 (17.2, 17)	13.1–23.1 (16.7, 73)	14.6–20.8 (17.8, 60)	12.7–17.7 (15.4, 24)
Length of second dorsal-fin base	10.9–12.6 (11.9, 16)	9.8–14.2 (12.1, 71)	11.4–15.9 (13.2, 57)	10.5–13.9 (12.4, 23)
Length of anal-fin base	9.8–12.2 (10.9, 21)	8.1–12.5 (10.9, 73)	10.5–14.1 (12.3, 57)	9.5–13.5 (11.1, 24)
Length of first dorsal-fin spine	10.3–12.7 (11.2, 13)	8.7–13.7 (11.2, 71)	9.7–15.0 (13.0, 59)	9.7–13.3 (11.5, 23)
Length of second dorsal-fin spine	13.1–15.7 (14.4, 24)	11.7–16.4 (14.3, 72)	13.9–18.0 (16.1, 57)	11.5–15.6 (13.9, 24)
Length of longest ray of second dorsal fin	6.6–10.0 (8.6, 19)	7.1–10.0 (8.5, 73)	8.0–12.2 (9.8, 60)	7.2–9.4 (8.3, 23)
Length of longest ray of anal fin	7.4–9.6 (8.6, 24)	6.2–10.7 (8.4, 73)	7.7–11.6 (9.5, 60)	6.7–9.5 (7.9, 24)
Pectoral-fin length	11.7–13.5 (12.9, 33)	10.8–14.3 (12.7, 72)	11.3–16.0 (13.4, 60)	10.5–12.6 (11.4, 24)
Pectoral-fin base length	4.1–5.0 (4.5, 24)	4.2–5.4 (4.8, 19)	4.6–5.5 (5.1, 33)	4.3–5.1 (4.5, 12)
Pelvic-fin spine length	7.6–9.5 (8.4, 13)	6.4–10.1 (8.4, 70)	5.6–11.6 (9.3, 58)	6.2–9.5 (8.1, 22)
Pelvic-fin length	10.2–11.6 (10.8, 26)	9.3–12.4 (10.6, 73)	9.8–12.8 (11.2, 59)	9.0–10.8 (9.9, 23)
Gill-raker length at angle	**7.6–9.1 (8.3, 29)**	**5.6–9.1 (7.3, 73)**	**7.3–10.1 (8.4, 56)**	**3.3–5.0 (4.2, 21)**
Measurements (in % of head length)				
Upper-jaw length	**54.4–60.0 (56.5, 36)**	**42.8–57.5 (50.4, 73)**	**47.2–63.8 (52.4, 60)**	**38.4–44.9 (41.9, 24)**
Counts				
Upper gill rakers	**17–20 (19, 60)**	**15–23 (20, 72)**	**14–20 (18, 56)**	**10–16 (13, 22)**
Lower gill rakers	**35–39 (36, 60)**	**33–41 (38, 71)**	**32–38 (35, 56)**	**21–24 (22, 20)**
Total gill rakers	**53–59 (56, 60)**	**49–64 (60, 71)**	**47–57 (53, 56)**	**32–38 (34, 20)**

Table 2. Proportional measurements expressed as % FL and gill-raker counts of the type specimens of nominal species of the genus *Rastrelliger*. Ranges are followed by sample sizes in parentheses.

	R. chrysozonus					*R. kanagurta*					*R. faughni*
				S. microlepidotus			*S. loo*	*S. moluccensis*	*S. reani*	*R. serventyi*	
	Lectotype SMF 487A	Paralectotype SMF 487B	[a] Paralectotype SMF 6781	Syntypes SMF 503	Syntype SMF 503	Neotype CAS SU 14594	Holotype MNHN 2910	Syntypes RMNH 6038	Syntype AMS B8140	Holotype WAM P. 181–001	Holotype USNM 190018
		$n = 1$	$n = 1$	$n = 2$	$n = 1$			$n = 2$	$n = 1$		
Fork length (FL, mm)	201.2	192.1	240.2	101.6–102.6 (2)	—	171.5	230.4	185.9–191.5 (2)	230.3	231.3	195.81
Measurements (in % FL)											
Head length	27.4	27.7	27.2	27.8–28.7 (2)	—	28.7	27.0	26.4–27.5 (2)	27.3	26.7	26.2
Snout length	7.7	7.6	7.0	7.0–7.8 (2)	—	9.0	8.0	6.8–7.2 (2)	8.0	7.9	6.6
Orbit diameter	67.2	6.6	6.3	7.4–8.0 (2)	7.6 [b]	6.1	7.2	6.4–6.7 (2)	7.5	7.0	7.9
Interorbital width	5.6	6.4	5.8	4.1–4.9 (2)	—	8.4	6.1	4.9–5.3 (2)	7.4	8.0	6.0
Snout to first dorsal-fin origin	35.6	35.3	35.6	34.3–36.3 (2)	—	36.6	35.4	34.7–35.0 (2)	37.0	36.7	34.3
Snout to second dorsal-fin origin	61.4	58.6	62.4	58.6–59.0 (2)	—	59.8	60.0	58.2–59.8 (2)	61.1	62.4	60.3
Snout to pectoral-fin base	28.2	28.4	28.0	27.9–29.5 (2)	—	30.0	29.4	26.5–28.3 (2)	28.3	28.6	26.5
Snout to pelvic-fin origin	33.0	33.5	34.0	31.5–32.2 (2)	—	34.9	34.5	30.5–31.2 (2)	34.8	34.4	30.8
Snout to origin of anal fin	62.5	62.2	63.8	60.0–60.9 (2)	—	60.1	62.5	59.3–60.6 (2)	64.5	63.7	61.9
Upper-jaw length	15.5	15.4	15.4	13.1–14.0 (2)	—	15.3	15.6	13.5 (2)	15.2	15.8	12.7
Head width	9.9	8.5	11.2	7.6–8.4 (2)	8.4 [b]	9.1	13.7	9.4–10.9 (2)	10.6	11.0	—
Body width	13.8	13.5	—	9.1–10.0 (2)	9.8 [b]	12.7	13.7	12.1–12.8 (2)	15.2	14.5	—
Body depth 1	21.9	22.0	25.0	19.0–19.1 (2)	—	21.9	20.7	19.2–21.3 (2)	22.4	24.4	—
Body depth 2	25.4	24.4	25.9	17.5–18.1 (2)	—	23.8	21.8	20.3–22.0 (2)	24.6	26.8	—
Body depth 3	24.6	24.9	26.0	17.9–18.4 (2)	17.1 [b]	22.6	21.8	20.4–22.2 (2)	24.0	25.8	—
Upper-peduncle length	25.0	25.4	23.0	23.9–25.3 (2)	26.6 [b]	24.8	23.0	25.2–26.6 (2)	25.2	26.2	—
Lower-peduncle length	25.3	25.0	24.1	24.0–24.3 (2)	24.4 [b]	24.0	23.4	26.0–28.7 (2)	25.0	24.8	—
Caudal-peduncle depth	—	—	—	—	—	3.7	—	—	—	—	—
Length of first dorsal-fin base	19.6	18.9	16.6	18.9–19.0 (2)	19.9 [b]	17.9	16.8	18.8–20.6 (2)	17.8	18.8	15.5
Length of second dorsal-fin base	11.3	12.4	13.4	11.7–12.5 (2)	11.1 [b]	12.5	11.8	11.6–11.9 (2)	13.0	13.1	11.3
Length of anal-fin base	10.2	11.3	9.6	10.5–11.1 (2)	11.0 [b]	11.1	10.9	11.2 (1)	11.1	11.1	—
Length of first dorsal-fin spine	9.7	11.6	10.2	10.4–11.4 (2)	11.3 [b]	11.0	—	—	11.1	11.9	12.6
Length of second dorsal-fin spine	13.8		—	15.1 (1)	—	15.5	—	—	14.9	15.9	—
Length of longest ray of second dorsal fin	9.1	9.1	—	8.5 (1)	8.2 [b]	9.7	7.5	—	8.8	9.5	—
Length of longest anal-fin	9.2	8.6	—	8.0 (1)	7.0 [b]	9.8	—	—	8.2	9.7	—
Pectoral-fin length	12.4	12.9	—	12.1 (1)	11.5 [b]	14.4	10.9	—	13.5	15.0	—
Pectoral-fin base length	4.9	4.9	—	—	—	4.8	—	—	—	—	—
Pelvic-fin spine length	7.5	7.7	—	7.8–7.9 (2)	7.8 [b]	8.1	—	—	8.9	8.3	—
Pelvic-fin length	10.5	10.8	—	9.5–10.4 (2)	10.0 [b]	12.2	—	—	11.7	11.3	11.3
Gill-raker length at angle	—	—	—	—	—	7.8	6.9	—	7.2	7.7	—

Table 2. *Cont.*

Measurements (in % head length)											
Upper-jaw length	56.8	55.5	56.9	47.2–48.7 (2)		53.4	57.9	49.3–51.2 (2)	55.6	59.1	48.5
Counts											
Upper gill rakers	21		—	20 (1)	—	18	—	20–22 (2)	21	15	11
Lower gill rakers	35	35	—	36 (1)	—	37	—	40–42 (2)	38	—	24
Total gill rakers	56	—	—	56 (1)	—	55	52	62 (2)	59	—	35

[a] Stuffed; [b] Raw measurements (mm).

Table 3. Frequency distribution of the number of gill rakers of the four *Rastrelliger* species.

	Upper gill rakers															Lower gill rakers															
	10	11	12	13	14	15	16	17	18	19	20	21	22	23		21	22	23	24	—	32	33	34	35	36	37	38	39	40	41	42
R. chrysozonus								4	16	27	14	1 [a]								—				4 [a]	18	16	16	8			
R. kanagurta						5	2	4	9 [b]	13	20	9	10	5						—		1	3	9	9	12 [b]	16	11	9	4	1
R. brachysoma					1	1	7	4	24	14	5									—	2	3	9	25	9	6	2				
R. faughni	1	4 [c]	4	9	4		1									4	8	6	3 [c]	—											
	Total gill rakers																														
	32	33	34	35	36	37	38	—	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64					
R. chrysozonus								—							5	6	13	15 [a]	9	11	2										
R. kanagurta								—			2	2		1	6	7	6 [b]	6	7	10	3	10	5	6	2	1					
R. brachysoma								—	1	1		3	7	6	15	9	8	4	2												
R. faughni	2	2	5	4 [c]	4	2	2	—																							

[a] includes lectotype [b] includes neotype [c] includes holotype.

Table 4. Estimates of evolutionary divergence over sequence pairs between *Rastrelliger* spp.: The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Analyses were conducted using the Kimura 2-parameter model in MEGA11 using a total of 652 positions. This analysis involved all 47 nucleotide sequences used in phylogenetic analyses (see Table S1).

	R. kanagurta	*R. brachysoma*	*R. faughni*	*R. chrysozonus*
R. kanagurta	—	—	—	—
R. brachysoma	0.0351	—	—	—
R. faughni	0.0779	0.0797	—	—
R. chrysozonus	0.0303	0.0403	0.0795	—

3.3. Systematic Part

3.3.1. Rastrelliger Jordan and Starks, 1908

Rastrelliger Jordan and Starks in Jordan and Dickerson, 1908 [8]: 607, type species *Scomber brachysoma* Bleeker, 1851 by original designation—Matsui 1967 [12]: 77; Collette & Nauen 1983 [2]: 46.

Diagnosis. Body fusiform, moderately compressed, maximum body depth 16–28% of FL. Body covered mainly with finely ctenoid scales, those behind head and below pectoral fins larger, cycloid, and more conspicuous than those covering rest of body, but not developed as corselet. Snout pointed. Mouth large, oblique. Posterior tip of lacrimal below or extending posteriorly beyond posterior edge of eye. Eye covered by adipose eyelid anteriorly and posteriorly. Both jaws with very small conical teeth; no teeth on vomer and palatine bone. Tiny villiform teeth on basibranchial posteriorly. Gill rakers varying from 21 to 41 on lower limb of first arch. First and second dorsal fins widely separated, first dorsal fin with VIII–XI spines, second usually with 12 soft rays, followed by 5 finlets. Anal fin with one rudimentary spine and usually 11–12 soft rays followed by 4–6 (usually 5) finlets. Pectoral fins short, usually with 19 or 20 rays. Interpelvic process small and single. Two small keels on each side of caudal peduncle at base of caudal-fin lobes, with no medial keel between them. Swimbladder present. Precaudal plus caudal vertebrae 13 + 18, total 31, including hypural. First interhaemal bone anterior to haemal spine of 14th vertebra. Last branchiostegal ray forming wide plate. Color when fresh typically bluish green to dark blue dorsally, with 1–3 rows of black spots along back, silvery ventrally, often with blackish to yellowish longitudinal stripes laterally.

Rastrelliger is distinguished from the most similar Scombroid genus *Scomber* by the following features: vomer and palatine teeth absent (vs. present in *Scomber*); first anal-fin spine rudimentary (vs. strong); first interhaemal bone anterior to haemal spine of 14th (vs. 15th) vertebra; and last branchiostegal ray forming wide plate (vs. only slightly flattened) [12]. The genus comprises four valid species, viz., *R. brachysoma* (Bleeker, 1851), *R. chrysozonus* (Rüppell, 1836), *R. faughni* Matsui, 1967, and *R. kanagurta* (Cuvier, 1816), generally distributed in the Indo-Pacific Oceans (Figure 2).

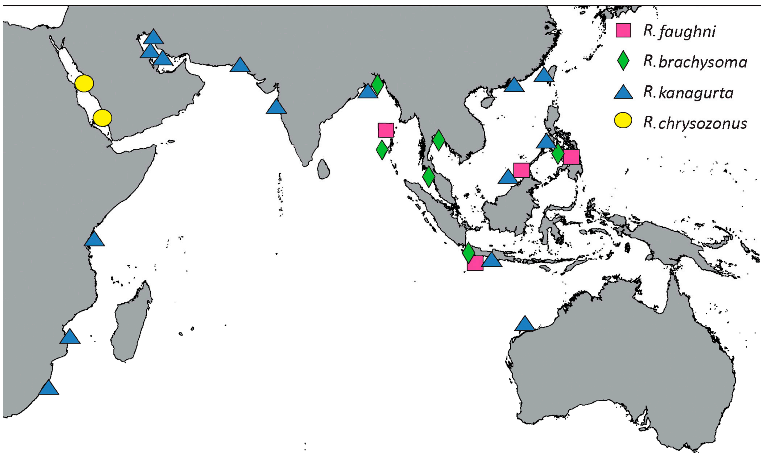

Figure 2. Sampling localities of the examined specimens of *Rastrelliger* spp.; entire distribution of each species is given in the text.

3.3.2. *Rastrelliger brachysoma* (Bleeker, 1851)

English name: Short Mackerel
(Figure 3; Tables 1 and 3)

Figure 3. *Rastrelliger brachysoma*, fresh specimen, UPVMI 169, 175.8 mm FL, Philippines, Panay Island, off Iloilo. Photo by the UPV Museum of Natural Sciences.

Scomber brachysoma Bleeker, 1851 [33]: 356 (type locality: Jakarta (Batavia), Java, Indonesia; holotype: RMNH.PISC. 6040).

Scomber neglectus van Kampen, 1907 [34]: 7 (type locality: Java, Indonesia; no types known)—de Beaufort 1951 [35]: 211 (Sumatra, description).

Rastrelliger brachysoma—de Beaufort, 1951 [35]: 210 (description of holotype); Boeseman 1964 [36]: plate 1, Figure 1 (photo of holotype); Jones and Silas 1964 [37]: 256 (Andaman Sea, description); Collette and Gibbs 1967 [17]: 25; Collette and Nauen 1983 [2]: 46 (Andaman Sea to Philippines, Papua New Guinea, and Fiji; description); Sirimontaporn 1984 [38]: 31, Figure 283 in (Songkhla, Thailand, list); Gloerfelt-Tarp and Kailola 1984 [39]: 259 (Indonesia; description); Wass 1984 [40]: 31 (Samoa Islands, listed); Mishra et al. 1999 [41]: 89 (Orissa, India, listed); Collette 2001 [1]: 3737 (western Pacific, description); Collette et al. 2001 [42]: 7 (key, followed Matsui 1967 [12]); Collette 2003 [43]: 6 (listed); Kimura 2009 [44]: 312 (southern Thailand, description); Seeto and Baldwin 2010 [45]: 27 (Fiji, listed); Satapoomin 2011 [46]: 69 (southwestern Thailand, listed); Rajan et al. 2013 [47]: 73 (Andaman and Nicobar Islands, listed); Kimura 2013a [48]: 204 (Gulf of Thailand, description); Larson et al. 2013 [49]: 218 (Northern Territory, Australia, listed); White et al. 2013 [50]: 326 (Indonesia); Basheer et al. 2015 [51]: 875 (Indian waters; phylogenetic analysis); Muto et al. 2016 [18]: 276 (Panay I., Philippines, genetic and morphological analysis); Hata 2017a [52]: 213 (Panay I., Philippines, description); Roul et al. 2017 [53]:

1 (Andaman Islands, length-weight relationship); Ali et al. 2018 [54]: 187 (Southeast Asia); Collette and Graves 2019 [3]: 89 (description); Psomadakis et al. 2020 [55]: 571 (Myanmar, distinctive characters); Muto et al. 2021 [56]: 2792 (South China Sea, phylogeography); Vilasri et al. 2023 [57]: 95, pl. 10B (Gulf of Thailand, listed, photograph); Hata et al. 2024 [58]: 205 (Philippines).

Material examined. 60 non-type specimens from off Iloilo, Panay Island, the Philippines, all purchased at a local fish market by an ichthyofaunal survey team jointly managed by UPVMI and KAUM: UPVMI-00169, 185.7 mm, 6 September 2012; UPVMI-00192, 191.0 mm, 7 September 2012; UPVMI-00358, 00375–00378, 157.3–171.1 mm, 19 December 2012; UPVMI-00638–00643, 00645–00651, 00654–00656, 00662–00696, 142.6–180.0 mm FL, 19 August 2013; UPVMI-01069, 01072, 165.0–177.4 mm, 29 July 2014.

Diagnosis. Dorsal-fin rays VIII–X (usually IX) + 11–13 + 5 (rarely 6) finlets; body deep, distance between origins of first dorsal and pelvic fins (body depth 2) 24.2–28.3% of FL; head length 25.5–29.3% of FL, subequal to body depth 2; snout to base of pectoral fin 26.8–29.8% of FL; caudal peduncle moderately deep, its depth 3.8–4.3% of FL; mouth large, upper jaw extending posteriorly to vertical at rear margin of eye, upper-jaw length 47.2–63.8% of head length; maxilla almost extending posteriorly to hind margin of lacrimal; gill rakers very long, visible from side when mouth open; gill rakers on first gill arch 14–20 on upper limb + 32–38 on lower limb = 47–57 (usually 50–56); length of gill raker at angle of gill arch 7.3–10.1% of FL; number of bristles on longest gill raker varying from 150 to 240; intestine very long, 3.2–3.6 times longer than FL; no narrow longitudinal stripe below longitudinal rows of black spots on dorsum.

Color when fresh (Figure 3). Grayish to greenish blue or yellowish green dorsally, silver ventrally, with 1–3 longitudinal rows of black spots above lateral line, sometimes indistinct or absent. Dorsal and pectoral fins yellowish to dusky, margins darker. Anal and pelvic fins white. Caudal fin dusky or dusky yellow, with black margin. All fins except for caudal fin semitranslucent. Black spot at upper pectoral-fin base. Faint black blotch sometimes behind tip of pectoral fin.

Distribution and habitat. In this study, *R. brachysoma* is observed in the Philippines (Panay Island) and Bangladesh (21°31′ N, 92°35′ E), India, the Gulf of Thailand, Malaysia, and Indonesia (West Java) based on specimens and molecular evidence (Figure 1). The species has also been recorded from the northern coast of Australia, Papua New Guinea, Fiji, and Samoa, in previous studies (see synonym list).

Morphological comparison. *Rastrelliger brachysoma* is diagnosed from all other congeners by having a deeper body, with the distance between the origins of the first dorsal and the pelvic fins tending to be longer than those of the other three species (24.2–28.3% of FL vs. 19.2–25.1% in the other three: Figure 4), and a deeper caudal peduncle (≥3.8% of FL vs. ≤3.8%). Moreover, the length of the second spine of the dorsal fin of *R. brachysoma* tends to be longer than that of the other three (13.9–18.0% of FL vs. ≤16.4%). The species also lacks the narrow golden to dark longitudinal stripes on the upper part of the body that the other congeners often possess.

Remarks. The diagnosis provided above is primarily based on the specimens from Panay Island, the Philippines. The number of bristles on the longest gill rakers and the length of the intestine followed Collette and Nauen (1983) [2].

Scomber brachysoma was originally described by Bleeker (1851) [33] on the basis of a single specimen from Jakarta, Indonesia. He noted the body depth of the specimen as 3 in its length. According to de Beaufort (1951) [35] who closely examined the specimen (= holotype of *S. brachysoma*), it is characterized by a great depth of 2.79 in its length (120 mm excluding the caudal fin), 6 dorsal and anal finlets, minute teeth on both jaws with no palatine teeth, and 15 and 35 rakers, respectively, on upper and lower limbs of the first gill arch. Boeseman (1964) [36] subsequently listed RMNH.PISC. 6040 as the holotype of the species, providing a photograph that shows the specimen's extremely high body, consistent with the descriptions by Bleeker (1851) [33] and de Beaufort (1951) [35].

The number of gill rakers and the dentition indicate that the holotype of *S. brachysoma* is a member of the genus *Rastrelliger* as presently recognized. Furthermore, the number of gill rakers and the body depth indicate that it is most likely conspecific with the specimens of *R. brachysoma* described herein, the latter being characterized by relatively few gill rakers and the deepest body among the species of the genus (Tables 2 and 4). Although the body depth of the holotype is even greater than the range of the present specimens, it is considered to be an intraspecific variation.

Scomber neglectus was described as a new species by van Kampen (1907) [34] from Java, Indonesia. Although it was thereafter recognized as another "deep bodied species" similar to *R. brachysoma* by several authors (e.g., de Beaufort 1951) [35]), Jones and Silas (1964) [37] synonymized it under *R. brachysoma*. Subsequently, Collette and Nauen (1983) [2] and Collette (2003) [43] also listed it as a synonym of *R. brachysoma* without explanation. Our review of the original description of *S. neglectus* confirmed that it is conspecific with *R. brachysoma* described herein, based on its relatively high body. Importantly, the body depth 2 of the specimen illustrated by van Kampen (1907) [34] (fig. B, no plate number given) is estimated to be 29% of FL, closely matching the present specimens of *R. brachysoma*. Therefore, we consider that *S. neglectus* van Kampen, 1907 is a junior synonym of *S. brachysoma* Bleeker, 1851.

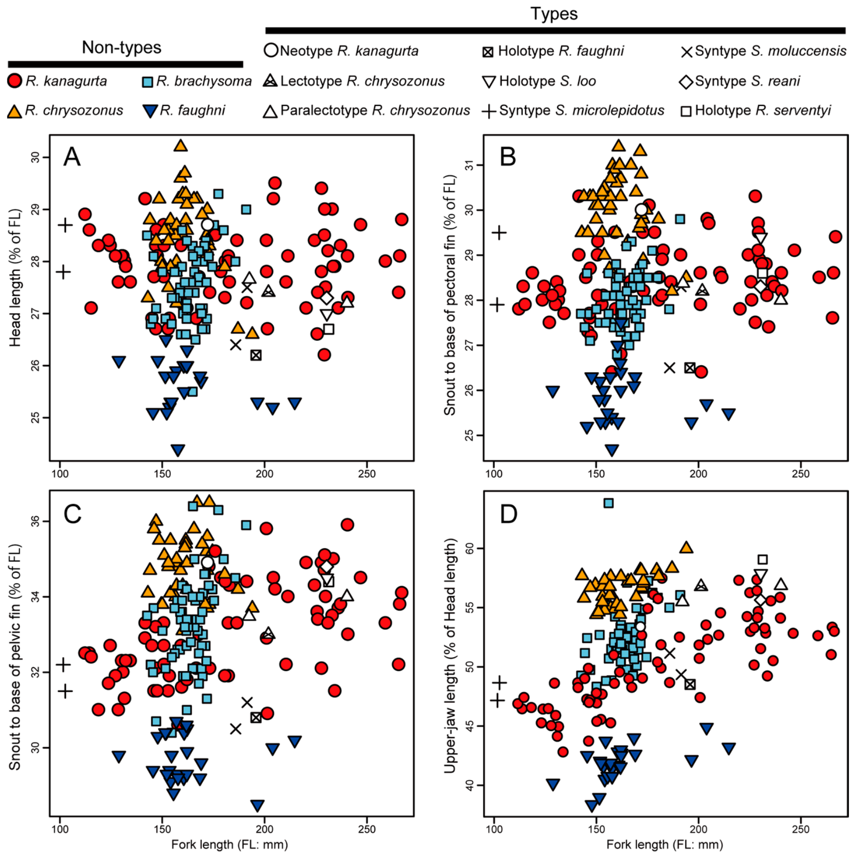

Figure 4. *Cont.*

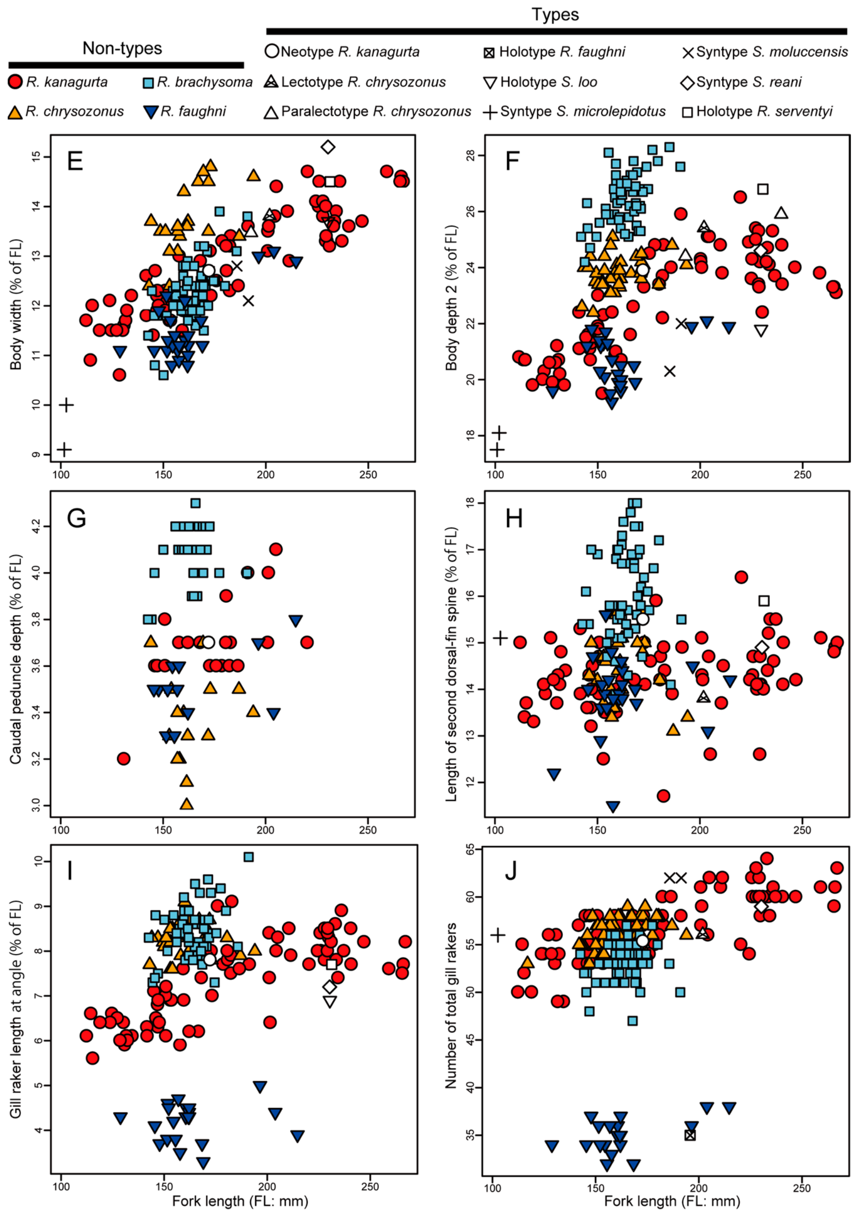

Figure 4. Selected measurements (in % of FL or % of head length) and meristics, plotted against FL, of four species of the genus *Rastrelliger*. (**A**) Head length; (**B**) Snout to pectoral-fin base; (**C**) Snout to pelvic-fin origin; (**D**) Upper-jaw length; (**E**) Body width; (**F**) Body depth 2; (**G**) Caudal peduncle depth; (**H**) Length of second dorsal-fin spine; (**I**) Gill-raker length at angle; (**J**) Number of total gill rakers.

3.3.3. Rastrelliger chrysozonus (Rüppell, 1836)

New English name: Golden-striped Mackerel
(Figures 5–8; Tables 1–3)

Scomber kanagurta (non Cuvier, 1816)—Rüppell 1828 [6]: 93 (Red Sea); Klunzinger 1871 [7]: 441 (Red Sea); Cuvier in Cuvier and Valenciennes, 1832 [59] (in part): 49 (Red Sea).

Scomber chrysozonus Rüppell, 1836 [60]: 37 (type locality: Massawa, Eritrea, Red Sea; 3 syntypes: SMF 487 (2), SMF 6781 (1); lectotype (designated herein): SMF 487)—Rüppell, 1852 [61]: 13; Dor 1984 [62]: 263 (invalid lectotype designation).

Scomber microlepidotus Rüppell, 1836 [60]: 38 (type locality: Massawa, Eritrea, Red Sea; 3 syntypes: SMF 503)—Rüppell, 1852 [61]: 13 (Red Sea); Klunzinger 1871 [7]: 443 (Red Sea).

Rastrelliger kanagurta (non Cuvier, 1816)—Bauchot & Blanc 1961 [63] (in part): 374 (Red Sea); Ben-Tuvia 1968 [64]: 35 (Eilat and Eritrea); Collette 1970 [65]: 4 (Red Sea and Israel, Mediterranean Sea); Tortonese 1983 [66]: 109 (Jeddah, Saudi Arabia); Collette and

Nauen 1983 [2] (in part): 48 (at least in Red Sea and western part of Gulf of Aden); Dor 1984 [62]: 263 (Red Sea, listed); Goren and Dor 1994 [67]: 70 (Red Sea, listed); Khalaf and Disi 1997 [68]: 201 (Jordan, description); Debelius 1998 [69]: 199 (Safaga, photographs); Khalaf 2004 [70]: 47 (Jordan, listed); Lieske and Myers 2004 [71]: 208 (Marsa Alam, photograph); Golani and Bogorodsky 2010 [13]: 52 (Red Sea, listed); Bogorodsky et al. 2014 [15]: 430 (off Jizan, Saudi Arabia); Golani and Fricke 2018 [14] (Red Sea, listed); Ryanskiy 2022 [72]: 119 (Marsa Nakari, Egypt, photographs).

Material examined. Type specimens (all from Massawa, Eritrea, Red Sea)—**Lectotype (designated herein):** SMF 487, 201.0 mm FL (Figure 5A). **Paralectotypes**, SMF 487, 191.5 mm FL (Figure 5B); SMF 6781, 240.0 mm (Figure 5C). **Other type specimens**: SMF 503, syntypes of S. microlepidotus, 3: 101.5–102.5 mm (Figure 5D–F). **Non-type materials**, all from Saudi Arabia, Red Sea (60 specimens): KAUMM 122 [KAU12-576], 6: 153.0–172.0 mm, RSS1-2012-Trawl 1, 21–22 m, off Jizan, 2012, coll. T.J. Alpermann et al.; KAUMM 123 [KAU12-667, 668 & 876–879], 8: 143.0–157.0 mm, RSS1-2012-Trawl 7, 21–22 m, off Jizan, 2012, coll. T.J. Alpermann et al.; KAUMM 480, 1: 160 mm, st 1, 10–12 m, RSS1-2014-Trawl 1 st 6, off Jizan, 31 October 2014, coll. T.J. Alpermann et al.; KAUMM 481, 8: 157.0–182.0 mm, RSS1-2017-1 st 10, 36–65 m, 30 January 2017, coll. S.V. Bogorodsky et al.; KAUMM 482, 1: 169.5 mm, RSS1-2017-1 st 1, 52–59 m, off Jizan, 25 January 2017, coll. S.V. Bogorodsky et al.; SMF 35077 [KAU12-664 to 666], 8: 146.0–161.5 mm, RSS1-2012-Trawl 1, 21–22 m, off Jizan, 2012, coll. T.J. Alpermann et al.; SMF 35078 [KAU12-575], 5: 142.0–187.0 mm, RSS1-2012-Trawl 7, 21–22 m, off Jizan, 2012, coll. T.J. Alpermann et al.; SMF 35928 [KAU14-1024], 1: 117.0 mm, RSS1-2014 st 45, 2 m, Al Lith, 17 November 2014, coll. S.V. Bogorodsky (from fisherman); SMF 35929 [KAU14-426], 1: 158.0 mm, RSS1-2014-Trawl 15 st 20, 40–50 m, off Jizan, 05 November 2014, coll. T.J. Alpermann et al.; SMF 35930 [KAU17-057], 12: 156.5–173.0 mm, RSS1-2017-1 st 15, 43–56 m, off Jizan, 31 January 2017, coll. S.V. Bogorodsky et al.; SMF 35931 [KAU17-096], 3: 167.0–194.0 mm, RSS1-2017-1 st 8, 21–23 m, off Jizan, 30 January 2017, coll. S.V. Bogorodsky et al.; SMF 35933, 6: 163.0–179.5 mm, RSS1-2017-1 st 10, 36–65 m, 30 January 2017, coll. S.V. Bogorodsky et al.

Figure 5. *Rastrelliger chrysozonus*, type specimens. (**A**) Lectotype of *Scomber chrysozonus*, SMF 487, 188.8 mm FL; (**B**) Paralectotype of *Scomber chrysozonus*, SMF 487, 179.0 mm FL; (**C**) Paralectotype of *Scomber chrysozonus*, SMF 6781, 225.3 mm FL; (**D**) Syntype of *Scomber microlepidotus*, SMF 503, 96.4 mm FL; (**E**) Syntype of *Scomber microlepidotus*, SMF 503, FL not available; (**F**) Syntype of *Scomber microlepidotus*, SMF 503, 96.1 mm FL.

Figure 6. *Rastrelliger chrysozonus*, SMF 35931 [KAU17-96], 194.0 mm FL, Red Sea, Saudi Arabia, off Jizan. (**A**) Head close-up; (**B**) Head close-up, posterior end of maxilla and lacrimal; (**C**) Side of body shows scale pattern. Photos by S.V. Bogorodsky.

Diagnosis. Dorsal-fin rays IX–X (usually IX) + 11–12 + 5 finlets; body moderately deep, distance between origins of first dorsal and pelvic fins 22.4–25.1% of FL; head length 26.6–30.2% of FL, longer than body depth; snout to base of pectoral fin 28.2–31.4% of FL; caudal peduncle moderately low, its depth 3.0–3.7% of FL; mouth large, upper jaw extending posterior to or little behind vertical at rear margin of eye, upper-jaw length 54.4–60.0% of head length; maxilla almost extending posteriorly to hind margin of lacrimal; gill rakers very long, visible from side when mouth open, gill rakers on first gill arch 17–21 + 35–39 = 53–59 (usually 55–58); length of gill raker at angle of gill arch 7.6–9.1% of FL; number of bristles on longest gill raker varying from 120 to 155; intestine 1.5–1.7 times longer than FL; narrow golden to dark longitudinal stripes below longitudinal rows of black spots on dorsum.

Figure 7. *Rastrelliger chrysozonus*, live individuals. (**A**) Red Sea, Egypt, Lahami Bay; (**B**) Red Sea, Egypt, Mangrove Bay. Photos by S.V. Bogorodsky.

Description. Measurements relative to FL and number of gill rakers are shown in Tables 1 and 3. Body moderately deep, little compressed laterally. Head moderately large, its length greater than body depth. Predorsal profile gently convex. Snout somewhat pointed, slightly longer than eye diameter. Anterior nostril a simple small opening, halfway between tip of snout and anterior margin of eye; posterior nostril slit-like, little curved. Eyes lateral; adipose eyelid covering most of eye, except a narrow slit at center of pupil, extending anteriorly over preorbital pit. Interorbital moderately wide, narrower than eye diameter. Mouth terminal, moderately large, slightly oblique, lower jaw slightly projecting. Rear margin of upper jaw slightly behind at vertical through posterior margin of eye. Maxilla mostly concealed by lacrimal when mouth closed (Figure 6A), posterior margin of maxilla almost extending to posterior margin of lacrimal (Figure 6B). Each jaw with tiny conical teeth, interspace between teeth broader than length of tooth; no vomerine and palatine teeth. Anterior margin of tongue rounded. No teeth on basibranchial anteriorly, patches of sharp villiform teeth medially posteriorly. Gill rakers slender, thin laterally and long, visible when mouth opened. Number of bristles on longest rakers varying from 120 to 155. Posterior margin of preopercle and opercle smooth, corner of each broadly rounded. Caudal peduncle low. Both small keels on caudal-fin base converging slightly posteriorly. Intestine 1.5–1.7 times longer than FL.

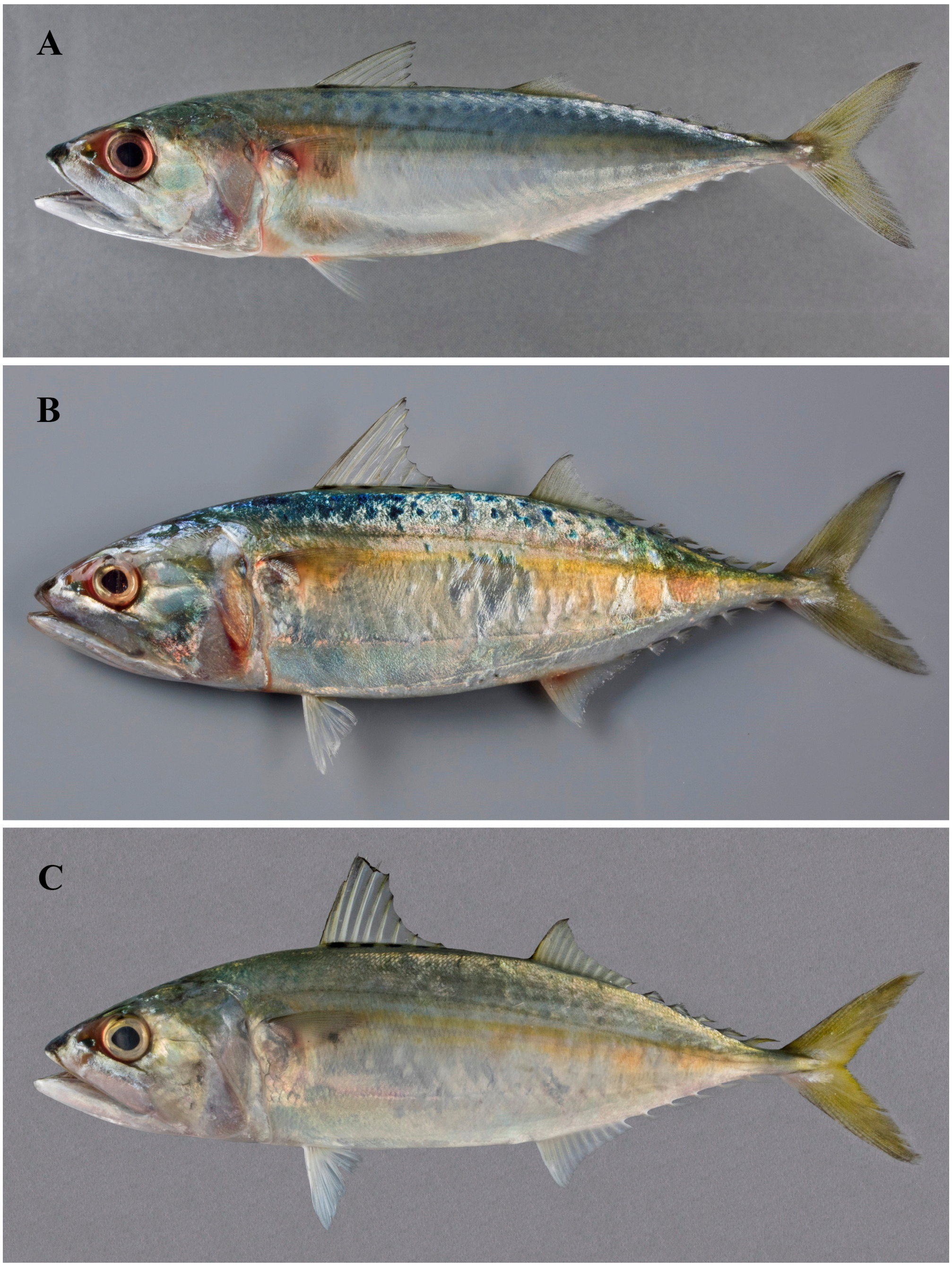

Figure 8. *Rastrelliger chrysozonus*, fresh specimens. (**A**) SMF 35928 [KAU14-1024], 117.0 mm FL, Red Sea, Saudi Arabia, Al Lith; (**B**) KAUMM 482, 169.5 mm FL, Red Sea, Saudi Arabia, Jizan; (**C**) SMF 35931 [KAU17-96], 194.0 mm FL. Photos by S.V. Bogorodsky.

Fins. Two separate dorsal fins, first with IX–X (usually IX) spines and 12 soft rays followed by 5 finlets; anal-fin rays 12–13 (usually 12) (except for first rudimentary spine) followed by 5 finlets; pectoral-fin rays 19–20. Base of first dorsal fin longer than base of second dorsal fin. First dorsal fin higher than second fin, second spine longest. First dorsal-fin origin behind vertical at pectoral-fin base; second dorsal-fin origin only one ray in advance of origin of anal fin. Soft rays of second dorsal fin progressively shorter from second to seventh ray, remaining rays subequal in length. Length of anal-fin base subequal to base of second dorsal fin. Pectoral fins semitriangular, short, extending posteriorly to below middle of first dorsal fin. Pelvic fins slightly shorter than pectoral fins, not reaching anus when depressed; origin of pelvic fin little in advance of origin of first dorsal fin. Caudal fin forked, shorter than head.

Scales. Body with small finely ctenoid scales, except for cycloid on nape and in area below pectoral-fin base where scales larger than on rest of body (Figure 6C). Several transverse rows of scales on breast at angle of opercle oriented diagonally backwards then in vertical rows from above origin of pelvic fins. Scales between lateral line and origin of first dorsal fin 8.5–9.5 except for rudimentary scales at base of dorsal fin. Predorsal scales nearly reaching to vertical through posterior edge of eye, ending in deep W shape. Lateral line simple, straight. Head mostly naked except for 3–4 rows of thin embedded cycloid scales on preopercle. Second dorsal and anal fins and basal part of pectoral fin scaled, other fins unscaled.

Color in life (Figure 7). Silvery blue-green dorsally, silvery on side and ventrally, sometimes with golden reflections; upper half of body with two or three rows of small blackish spots along back and four or five narrow stripes below, dorsal two stripes blackish, ventral two or three stripes dark golden with reflection, lowermost faint stripe preceded by one or rarely two black spots at posterior margin of pectoral fin at level of lower half of pectoral-fin base, size of first spot subequal to pupil. Fins except for caudal with pale grey spines and rays and semitranslucent membranes; caudal fin bluish grey.

Color when fresh (Figure 8). Similar to color in life but stripes becoming pale golden and caudal fin grey with yellowish hue in fresh specimens; black spot in preorbital pit becoming visible through adipose eyelid.

Etymology. The name chrysozonus is in reference to having golden stripes on the side of the body [60].

Distribution and habitat. Restricted to the Red Sea. Records of *Rastrelliger* from the western part of the Gulf of Aden, Djibouti [73], from Socotra [74] and Somalia [75] require investigations to determine whether they are *R. chrysozonus* or *R. kanagurta*. There are no documented records of *Rastrelliger* from southern and central Oman. The photograph in the book on coastal fishes of Oman [76] was in fact taken in India.

Occurs in schools of variable size, mainly in protected coastal waters where plankton are abundant; reported from nearly surface to depth of 70 m; feeds by swimming with mouth wide open and operculum flared through concentrations of plankton.

Morphological comparison. Rastrelliger chrysozonus is distinguished from R. kanagurta by having a longer upper jaw (54.4–60.0%, mean 56.5%) of head length (vs. 42.8–57.5%, mean 50.4% in *R. kanagurta*). Furthermore, distances from the snout to the base of the pectoral fin and to the origin of the pelvic fin, body depth, and body width of R. chrysozonus tend to be slightly greater than those of R. kanagurta (Table 1; Figure 4). Comparisons of R. chrysozonus with R. brachysoma and R. faughni are given in "Morphological comparison" under each species.

Remarks. In his first book, Rüppell (1828) [6] described the Red Sea specimens of *Scomber kanagurta*. Subsequently, in another book, Rüppell (1836) [60] stated that mackerels from the Red Sea were distinct from *S. kanagurta*. He described two species based on materials from Massawa, Eritrea; *Scomber chrysozonus* (in p. 37) and *Scomber microlepidotus* (in p. 38). He separated them by body depth: body depth of $3^{1/2}$ in body length in *S. chrysozonus* and $4^{1/2}$ in *S. microlepidotus*. Dor (1984) [62] noted that a single lectotype SMF 487 was selected by Klausewitz for R. chrysozonus, and another specimen SMF 6781 was designated as a paralectotype. This type status was followed by Fricke et al. (2024) [77]. However, during the examination of type materials in the Senckenberg Museum Frankfurt by the third author of the present study, two specimens were found under the same catalog number SMF 487. Therefore, Dor's (1984) [66] lectotype designation is considered ambiguous and invalid according to ICZN Art. 74.5. To ensure nomenclatural stability, we designate the larger specimen (188.8 mm SL, 201.2 mm FL) from the two ethanol-preserved specimens under SMF 487 as the lectotype of R. chrysozonus, the second specimen (179.0 mm SL, 192.1 mm FL) under SMF 487 becoming one of two paralectotypes, together with the dried specimen SMF 6781. Rüppell (1836) [60] illustrated a single specimen of R. chrysozonus to accompany the original description of the species. However, we could not exclusively attribute it to any of the existing type specimens.

Examination of type specimens of the two nominal species described from the Red Sea, *S. chrysozonus* and *S. microlepidotus*, revealed that both are morphologically indistinguishable from the species recognized herein from the Red Sea (Figure 4, Tables 1–3), and are thus regarded as conspecific. Therefore, *Rastrelliger chrysozonus* is the valid name for this species, and *R. microlepidotus* becomes a junior synonym of the former. The synonymy of *R. microlepidotus* with *R. chrysozonus* may be explained that Rüppell (1836) [60] confused allometry in body depth with an interspecific difference. Rüppell (1836) [60] described *R. chrysozonus* based on large adults (192.1–240.2 mm FL), whereas juveniles (101.5–102.5 mm FL) were used for the description of *R. microlepidotus*. He distinguished the two species by relative body depth, which is herein shown to change with growth (Figure 4).

3.3.4. *Rastrelliger faughni* Matsui, 1967

Island Mackerel

(Figure 9; Tables 1–3)

Rastrelliger faughni Matsui, 1967 [12]: 74 (type locality: Oyster Inlet, Ulugan Bay, Palawan, the Philippines; holotype: USNM 190018)—Collette and Nauen 1983 [2]: 47 (description); Lewis et al. 1983 [78]: 4 (Fiji); Ni and Kwok 1999 [79]: 146 (Hong Kong, listed); Collette 2001 [1]: 3738 (western Pacific, description); Collette et al. 2001 [42]: 7 (key, followed Matsui 1967 [12]); Collette 2003 [43]: 6 (listed); Shao et al. 2008 [80]: 264 (southern Taiwan, listed); Seeto and Baldwin 2010 [45]: 27 (Fiji, listed); Satapoomin 2011 [46]: 69 (southwestern Thailand, listed); Rajan et al. 2013 [47]: 73 (Andaman and Nicobar Islands, listed); Larson et al. 2013 [49]: 218 (Northern Territory, Australia, listed); White et al. 2013 [50]: 328 (Indonesia); Basheer et al. 2015 [51]: 875 (Indian waters, phylogenetic analysis); Muto et al. 2016 [18]: 276 (Panay I., Philippines, genetic and morphological analysis); Hata 2017b [81]: 213 (Panay I., Philippines, description); Roul et al. 2017 [53]: 1 (Andaman Islands, length-weight relationship); Ali et al. 2018 [54]: 187 (Southeast Asia); Collette and Graves 2019 [3]: 93 (description); Psomadakis et al. 2020 [55]: 572 (Myanmar, distinctive characters); Muto et al. 2021 [56]: 2792 (South China Sea, phylogeography); Hata et al. 2024 [58]: 205 (Taiwan).

Scomber australasicus (not of Cuvier)—de Beaufort 1951 [35]: 206, Figure 35 (Buton Is., southeast of Sulawesi, Indonesia, description).

Material examined. **Holotype**: USNM 190018, 195.81 mm, Ulugan Bay, Palawan, the Philippines, 28 December 1908. **Non-type materials**: 24 specimens from Panay Island, the Philippines, all purchased at a local fish market by an ichthyofaunal survey team jointly managed by UPVMI and KAUM: UPVMI-00756, 00757, 00763, 145.6–148.4 mm, 20 August 2013; UPVMI-00987–00993, 145.6–169.0 mm, 28 July 2014; UPVMI-01310, 128.8 mm, 2 August 2014; UPVMI-01748–01751, 01753–01755, 01759, 01763, 01764, 145.5–214.7 mm, 26 February 2015.

Diagnosis. Dorsal-fin rays IX–X (usually X) + 11–13 + 5 (rarely 6) finlets; body slender, distance between origins of first dorsal and pelvic fins 19.2–22.1% of FL; head longer than body depth, its length 24.4–26.5% of FL; snout to base of pectoral fin 24.7–27.5% of FL; caudal peduncle moderately low, its depth 3.3–3.8% of FL; mouth moderately large, upper jaw nearly extending posteriorly to vertical at posterior edge of eye, upper-jaw length 38.4–44.9% of head length; maxilla not extending posteriorly to hind margin of lacrimal, its length about three-fourth of lacrimal length; gill rakers relatively short, not visible from side when mouth open, gill rakers on first gill arch 10–16 + 21–24 = 32–38 (usually 34–36), length of gill raker at angle of gill arch 3.3–5.0% of FL; number of bristles on longest gill raker varying from 30 to 55; intestine short, shorter or subequal to FL; faint narrow yellow to dark longitudinal stripe sometimes below longitudinal rows of black spots.

Color when fresh (Figure 9). Body and head greenish blue to greyish blue dorsally, silver ventrally. One to three longitudinal rows of black spots above lateral line, its size smaller than half of pupil diameter, sometimes united diagonally, forming vermiculation. One or two faint narrow yellow to dark longitudinal stripes sometimes below longitudinal rows of black spots. All fins except for caudal fin semitranslucent, white to dusky, sometimes yellowish; caudal fin dusky yellow. Black spot at upper pectoral-fin base. Faint black blotch sometimes behind tip of pectoral fin.

Distribution and habitat. In this study, *R. faughni* is observed from India, Indonesia (Java), Malaysia (Sabah), and the Philippines (Panay Island) based on specimens and molecular evidence. The species is also known from the Andaman Islands and the western coast of Thailand east through northern Australia, China, Taiwan, and Papua New Guinea to Fiji [1–3,58].

Morphological comparison. *Rastrelliger faughni* is easily distinguished from all other congeners by having fewer gill rakers (total gill rakers $\leq$ 38 in *R. faughni* vs. $\geq$47 in other congeners), a shorter gill raker at an angle ($\leq$5.0% of FL vs. $\geq$5.6%), a smaller head (24.4–26.5% of FL vs. $\geq$25.5% (mostly >26%)), distances from snout to pectoral-fin base (24.7–27.5% of FL vs. $\geq$26.4%), and to pelvic-fin origin (28.5–30.7% of FL vs. $\geq$30.4%), and lacrimal ($\leq$11.3% of FL vs. $\geq$10.4%). The species also differs from other congeners in that the black spots arranged in longitudinal rows above the lateral line are often united diagonally, forming vermiculated markings (vs. spots sometimes united longitudinally but rarely diagonally).

Figure 9. *Rastrelliger faughni*, KAUM-I 80695, 170.4 mm FL, Philippines, Panay Island, off Tigbauan. Photo by the Kagoshima University Museum.

Remarks. The diagnosis provided above is primarily based on the specimens from Panay Island, the Philippines, all of which were subjected to the genetic analysis. The number of bristles on the longest gill rakers and the length of the intestine followed Collette and Nauen (1983) [2].

de Beaufort (1951) [35] identified two scombrid specimens from Buton Island, Indonesia, as *Scomber australasicus*. Nonetheless, he noted his doubt about his identification: the specimens possessed a very weak anal-fin spine, attributable to the genus *Rastrelliger* rather than *Scomber.* Subsequently, Matsui (1967) [12] considered that de Beaufort's (1951) [35] specimens represented an undescribed species. He described a new species, *Rastrelliger faughni*, based on the specimens from the Philippines and Taiwan, which he believed to be conspecific with de Beaufort's (1951) [35] specimens. Matsui (1967) [12] characterized his new species primarily by relatively few and short gill rakers, and a slender body, closely resembling the species of *Scomber*. Notwithstanding, osteological observations by Matsui (1967) [12] confirmed that the new species was more closely related to *R. kanagurta* and *R. brachysoma* than to the species of *Scomber*. Therefore, he placed his new species in the genus *Rastrelliger*, leading to the redefinition of the genus.

Auxis pelei was originally described by Griffith and Smith (1834) [82] based on a single specimen from an unknown locality, accompanied by a color illustration (pl. 54). Fricke et al. (2024) [77] considered it to be a senior synonym of *R. faughni*, but gave precedence to *R. faughni* in accordance with ICZN Art. 23.9, because *A. pelei* had not been used as valid since 1899. Our examination of the original description, however, revealed that the specimen of *A. pelei* figured by Griffith and Smith (1834) [82] is a member of the genus *Auxis* as presently recognized. The specimen is characterized by an elongate body, widely separated first and second dorsal fins, eight dorsal finlets, seven anal finlets, and a corselet, being a combination of characters unique to the genus *Auxis* [1,83]. However, *A. pelei* cannot be identified with certainty to any known species of the genus, due to the lack of type specimens and the inadequate description. The figured specimen's scaleless area above the lateral line extends anteriorly beyond a vertical through the tip of the pectoral fin, attributable to both *Auxis thazard* and *A. brachydorax*. Although the latter two species are distinguishable from each other by geographic distributions, number of gill rakers, and corselet width under the second dorsal fin, none of these features are available for the specimen of *A. pelei*. Therefore, *A. pelei* is here regarded as *nomen dubium*.

3.3.5. *Rastrelliger kanagurta* (Cuvier, 1816)

Indian Mackerel

(Figures 10–13; Tables 1–3)

Kanagurta (non-binomial) Russell, 1803 [5]: 28, pl. 136 (one specimen, Vizagapatam, India; description, figure. Specimen not found).

Scomber kanagurta Cuvier, 1816 [4]: 313 (original locality: Vishakhapatnam (currently Vizagapatam), India, based on pl. 136 (figure of "kanagurta") of Russell 1803 [5] (= holotype by monotypy); type locality, Kozhikode, Kerala, India, based on newly designated neotype)—Cuvier in Cuvier and Valenciennes, 1832 [59] (in part): 49 (Pondicherry (Puducherry) and Malabar coast, India, description and reference to Russell's (1803) [5] pl. 136).

Scomber canagurta [sic]: Cuvier 1829 [84]: 197 (incorrect subsequent spelling; Vishakhapatnam (Vizagapatam), India).

Scomber loo Lesson, 1829 [85]: 277 (type locality: Port Praslin, New Ireland I., Bismarck Archipelago; holotype: MNHN 2910)—Cuvier in Cuvier and Valenciennes, 1832 [59]: 52 (Port Praslin, New Ireland I., Bismarck Archipelago).

Scomber delphinalis Cuvier in Cuvier and Valenciennes, 1832 [59]: 53 (type locality: Fort Dauphin, Madagascar; no types known).

Scomber moluccensis Bleeker, 1856 [86]: 40 (type locality: Ambon I., Molucca Is., Indonesia; 2 syntypes: RMNH.PISC 6038).

Scomber reani Day, 1871 [87]: 690 (type locality; Andaman Is., eastern Bay of Bengal; 3 syntypes: AMS B. 8140, ZSI 1841, ZSI B 109).

Scomber lepturus Agassiz, 1874 [88] (type locality: unknown; no types known).

Rastrelliger serventyi Whitley, 1944 [89]: 268 (type locality: Port Hedland, Western Australia; holotype: WAM P. 181-001).

Rastrelliger chrysozonus (non Rüppell)—Kishinouye 1915 [90]: 3 (Amami-oshima Island, Ryukyu Archipelago, Japan); Kishinouye 1923 [91]: 406, Figure 23 (southern China; Formosa (Taiwan); Truck Islands (Chuuk Lagoon), Caroline Islands)

Rastrelliger kanagurta—Bauchot & Blanc 1961 [62] (in part): 374 (Malabar coast and Pondicherry, India); Smith and Smith 1963 [92]: 41 (Seychelles, description); Kuronuma and Abe 1972 [93]: 104, pl. 17 (Persian/Arabian Gulf); Yamakawa 1979 [94]: 43 (Okinawa Island, Ryukyu Archipelago, Japan); Collette and Nauen 1983 [2] (in part): 48 (Indo-West Pacific; description); Sirimontaporn 1984 [38]: 31, Figure 284 (Songkhla, Thailand, list); Gloerfelt-Tarp and Kailola 1984 [39]: 259 (Indonesia, description); Wass 1984 [40]: 31 (Samoa, listed); Bianchi 1985 [95]: 119 (Tanzania); Kuronuma and Abe 1986 [96]: 232, pl. 26 (Kuwait); Randall and Anderson 1993 [97]: 41 (Maldives, listed); de Bruin et al. 1995 [98]: 317 (Sri Lanka); Randall 1995 [76]: 374 (Oman, description, photo from India); Randall et al. 1997 [99]: 448 (Great Barrier Reef, description); Nakamura 1997 [100]: 657 (Iriomote-jima Island, Ryukyu Archipelago, Japan); Fricke 1999 [101]: 56 (Reunion; invalid lectotype designation: see Remarks); Johnson 1999 [102]: 751 (Queensland, listed); Mishra et al. 1999 [41]: 89 (Orissa, India, listed); Myers 1999 [103]: 278 (Palau, description); Ni and Kwok 1999 [79]: 146 (Hong Kong, listed); Pereira 2000 [104]: 16 (Mozambique, listed); Collette 2001 [1]: 3739 (western Pacific, description); Collette et al. 2001 [42]: 7 (key, followed Matsui 1967 [12]); Hutchins 2001 [105]: 45 (Western Australia, listed); Collette 2003 [43]: 6 (listed); Adrim et al. 2004 [106]: 127 (Anambas Island, listed); Heemstra and Heemstra 2004 [107]: 416 (South Africa, description); Randall et al. 2004 [108]: 30 (Tonga, listed); Randall 2005 [109]: 611 (South Pacific, description, photograph from Indonesia); Randall et al. 2005 [110]: 131 (Marshall Islands, description); Senou et al. 2006 [111]: 89 (Ie-jima Island, Ryukyu Archipelago, Japan); Shao et al. 2008 [80]: 264 (southern Taiwan, listed); Fricke et al. 2009 [112]: 112 (Reunion, listed); Kimura 2009 [44]: 312 (southern Thailand, description); Motomura et al. 2010 [113]: 230 (Yaku-shima Island, Japan, listed); Seeto and Baldwin 2010 [45]: 27 (Fiji, listed); Fricke et al. 2011 [114]: 442 (New Caledonia, listed); Kimura 2011 [115]: 221 (Terengganu, Malaysia, description); Satapoomin 2011 [46]: 69 (southwestern Thailand, listed); Allen and Erdmann 2012 [116]: 1041 (East Indies, description, photo from Solomon Islands); Larson et al. 2013 [49]: 218 (Northern Territory, Australia, listed); Rajan et al. 2013 [47]: 73 (Andaman and Nicobar Islands, listed); White et al. 2013 [50]: 328 (Indonesia); Kimura et al. 2013b [117]: 204 (Gulf of Thailand, description); Chiang et al. 2014 [118]: 296 (eastern Taiwan); Fricke et al. 2014 [119]: 187 (Madang District, Papua New Guinea, listed); Basheer et al. 2015 [51]: 875 (Indian waters; phylogenetic analysis); Hata et al. 2015 [120]: 161 (Kagoshima Pref., Japan; Kota Kinabalu, Sabah, Malaysia; Kuala Terengganu, Terengganu, Malaysia; Gulf of Thailand; Rayong, Thailand; description); Kimura 2015 [121]: 87 (Johor, Malaysia, description); Psomadakis et al. 2015 [122]: 315 (Pakistan); Hata and Motomura 2016 [123]: 327, Figure 1 (Shimokoshiki Island, Tanega-shima Island, and mainland of Kagoshima Pref., southern Japan; description); Muto et al. 2016 [18]: 276 (Panay I., Philippines, genetic and morphological analysis); Hata 2017c [124]: 214 (Panay I., Philippines, description); Hata 2017d [125]: 262 (Kagoshima Bay, Kagoshima Pref., southern Japan); Sukumaran et al. 2017 [126] (India, genetic structure); Nakae et al. 2018 [127]: 335 (Amami-oshima Island, Ryukyu Archipelago, Japan); Hata 2018a [128]: 430 (Uchinoura Bay, Kagoshima Pref., southern Japan; description); Inaba 2018 [129]: 393 (Amami-oshima Island, Ryukyu Archipelago, Japan); Fricke et al. 2018 [130]: 362 (Madagascar, listed); Kimura 2018 [131]: 277 (Ha Long Bay, Vietnam and Johor Strait, Malaysia; description); Ali et al. 2018 [54]: 187 (Southeast Asia); Hata 2018b [132]: 1176 (southwestern Taiwan; description); Collette and Graves 2019 [3]: 97 (description); Eagderi et al. 2019 [133]: 104 (Persian/Arabian Gulf, listed); Ludt et al. 2020 [134]: 7 (United Arab Emirates, genetic analysis); Psomadakis et al. 2020 [55]: 572 (Myanmar, distinctive characters); Hata 2020a [135]: 511 (Uchinoura Bay, Kagoshima Pref., southern Japan); Hata 2020b [136]: 1176 (southwestern Taiwan; description); Shimose and Imai 2021 [137]: 11, Figure 1B,D (Ishigaki-jima Island, Ryukyu

Archipelago, Japan); Uehara et al. 2021 [138]: 132, Figure 2 (reproductive patterns and early life history; Nakagusuku Bay, Okinawa-jima Island, Ryukyu Archipelago, Japan); Collette 2022 [139]: 279 (Western Indian Ocean, description); Hata 2022 [140]: 283 (western coast of Satsuma Peninsula, Kagoshima Pref., southern Japan); Motomura 2023 [141]: 221 (Tanega-shima Island, Osumi Islands, Kagoshima Pref., Japan); Vilasri et al. 2023 [57]: 95, Pl. 10B (Gulf of Thailand, listed, photograph); Hata et al. 2024 [58]: 205 (Japan, East China Sea, Taiwan, Philippines, Palau, and Indonesia); Honda et al. 2024 [142]: 202, Figure 11B (Sagami Bay, Kanagawa Pref., Japan).

Rastrelliger brachysoma (non Bleeker)—Kamohara 1965 [143]: 34 (Okinawa Island, Ryukyu Archipelago, Japan).

Rastrelliger canagurta [sic]: Yoshino et al. 1975 [144]: 90 (Ryukyu Archipelago, Japan).

Material examined. Neotype: CAS 248440, 158.61 mm SL, Kozhikode, Kerala, India, coll. by Albert W. Herre, 14 January 1941 (Figure 10A). **Other type specimens**: RMNH.PISC 6038, 2 specimens, syntypes of *S. moluccensis*, 185.9–191.5 mm, Ambon Island, Molucca Islands, Indonesia, coll. by P. Bleeker (Figure 10B,C); AMS B. 8140, syntype of *S. reani*, 230.3 mm, coll. by F. Day (Figure 10D); WAM P. 181-001, holotype of *R. serventyi*, 231.3 mm, 20°18′ S, 118°35′ E, Port Hedland, Western Australia, October 1914, coll. by W.B. Alexander (Figure 10E); MNHN 2910, holotype of *S. loo* Lesson, 1829, 230.4 mm, Port Praslin, New Ireland Island, Bismarck Archipelago, coll. by R.P. Lesson and P. Garnot (Figure 10F). **Non-type materials**: CAS-SU 14594 (5), 171.5–182.1 mm, Kozhikode, Kerala, India, 14 January 1941, coll. by A.W. Herre; 66 specimens from Panay Island, the Philippines, all purchased at a local fish market by an ichthyofaunal survey team jointly managed by UPVMI and KAUM: SAIAB 89952, 202.5 mm, Tanzania (used only for color description and length of upper jaw); UPVMI-00357, 00359–00369, 209.8–239.8 mm, 19 December 2012; UPVMI-00644, 00652, 00653, 158.5–181.6 mm, 19 August 2013; UPVMI-00706–00710, 00758–00762, 146.3–232.3 mm, 20 August 2013; UPVMI-01068, 01070, 01071, 01073–01079, 167.3–266.3 mm, 29 July 2014; UPVMI 01297–01309, 01311–01313, 111.6–150.0 mm, 2 August 2014; UPVMI 01746, 01747, 01752, 01756–01758, 01760–01762, 01765, 141.0–200.7 mm; 26 February 2015; UPVMI 01954–01957, 228.5–246.2 mm.

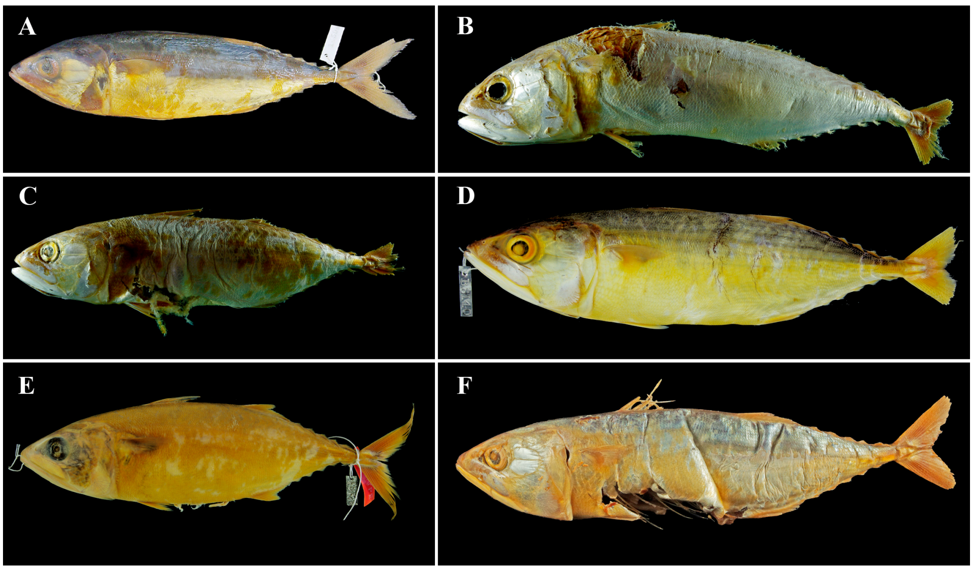

Figure 10. Type specimens of nominal species herein identified as *Rastrelliger kanagurta*. (**A**) Neotype of *R. kanagurta* Cuvier, 1816, CAS 248440, 158.6 mm FL, India, Kerala; (**B**,**C**) Syntypes of *Scomber moluccensis*, RMNH.PISC 6038, (**B**) 175.4 mm FL, (**C**) 182.2 mm SL; (**D**) Syntype of *Scomber reani*, AMS B. 8140, 220.9 mm FL; (**E**) Holotype of *Rastrelliger serventyi*, WAM P. 181-001, 224.5 mm FL; (**F**) holotype of *Scomber loo* Lesson, 1829, MNHN 2910, 230.4 mm FL.

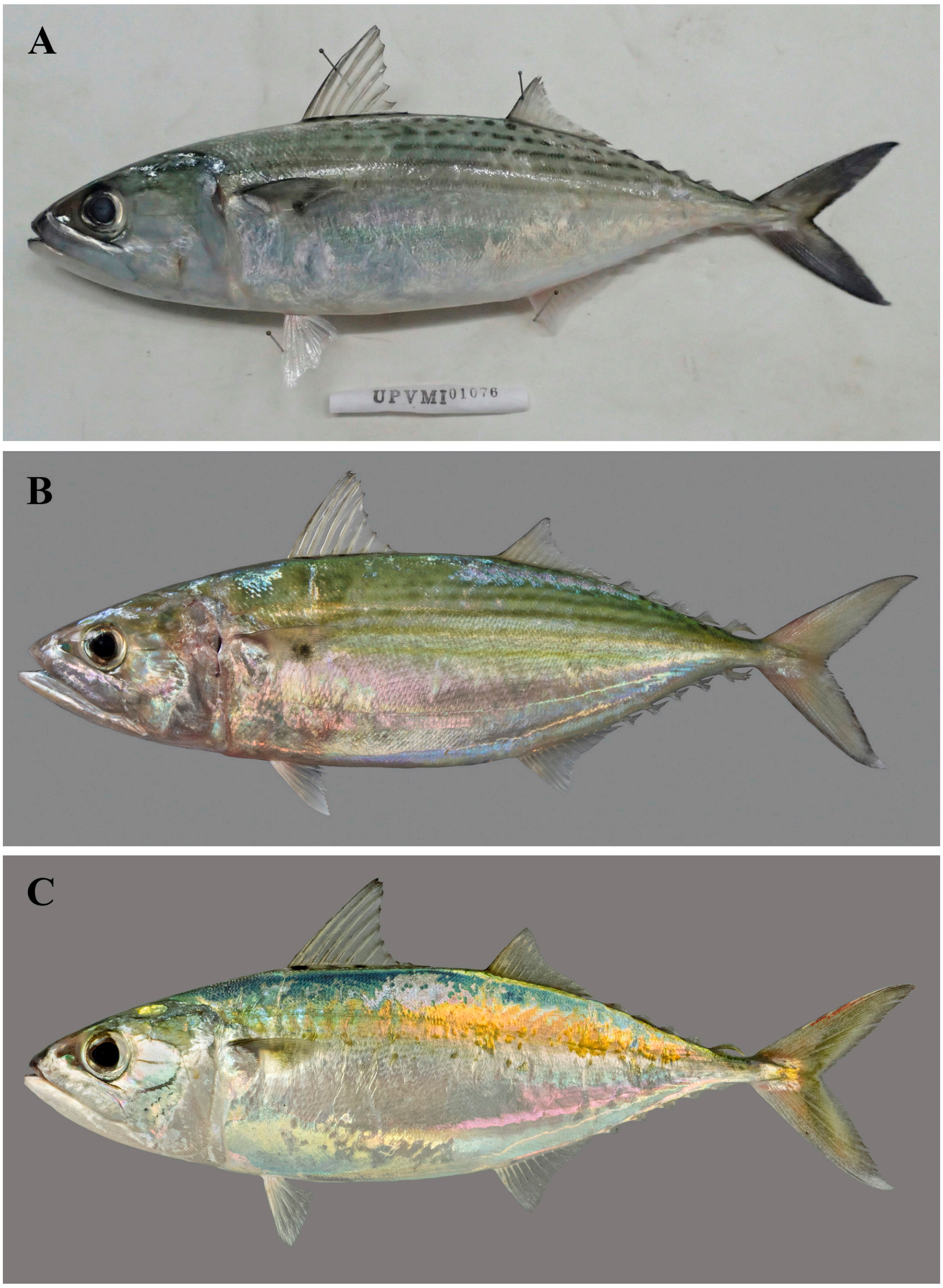

Figure 11. *Rastrelliger kanagurta*, fresh specimens. (**A**) UPVMI 01076, 265.3 mm FL, Philippines, Panay Island, off Iloilo; (**B**) Uncatalogued [tissue sample QG17-103], Persian/Arabian Gulf, Qatar; (**C**) SAIAB 89952 [tissue sample SPR22-571], 210.0 mm FL. Photos (**A**) by N. Muto, (**B**,**C**) by FAO_EAF-Nansen Programme, S.V. Bogorodsky.

Diagnosis. Dorsal-fin rays VIII–X (usually IX) + 11–13 + 5 (rarely 6) finlets; body moderately deep, distance between first dorsal and pelvic fins 19.5–26.5% of FL; head length 26.2–29.5% of FL, longer than body depth; snout to pectoral-fin base 19.5–26.5% of FL; caudal peduncle low, its depth 3.2–4.1% of FL; mouth large, upper jaw extending posteriorly to vertical at rear margin of eye, upper-jaw length 42.8–57.5% of head length; maxilla almost extending posteriorly to hind margin of lacrimal; gill rakers very long, visible from side when mouth open, gill rakers on first gill arch 15–23 + 33–42 = 49–64 (usually 53–62), length of gill raker at angle of gill arch 5.6–9.1% of FL; number of bristles on longest gill raker varying from 105 to 160; intestine 1.4–1.8 times longer than FL; narrow golden to dark longitudinal stripes below longitudinal rows of black spots on dorsum.

Figure 12. *Rastrelliger kanagurta*, alive individuals, Indonesia, Raja Ampat Islands. Photo by G.R. Allen.

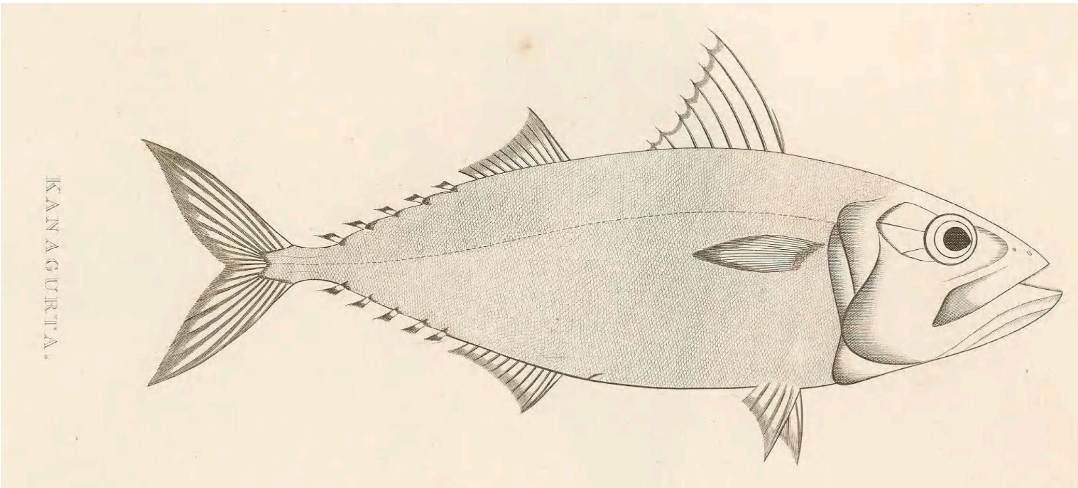

Figure 13. Drawing by P. Russell (1803) [5], 10 inches (ca. 254 mm) total length, being the basis for the original description (=the holotype) of *Scomber kanagurta* Cuvier, 1816.

Description. Measurements relative to FL and number of gill rakers are shown in Tables 1 and 3. Body moderately deep, compressed laterally. Head moderately large, longer than body depth. Predorsal profile gently convex. Snout somewhat pointed, slightly longer than eye diameter. Posterior nostril slit-like, curved, situated at anterior margin of adipose eyelid; anterior nostril a simple small opening, above halfway between tip of snout and anterior margin of eye. Eyes lateral; adipose eyelid covering most of eye, except narrow slit at center of pupil, extending anteriorly over preorbital pit. Interorbital moderately wide. Mouth terminal, moderately large, slightly oblique, lower jaw slightly protruding. Posterior margin of upper jaw ending posteriorly slightly behind vertical through posterior margin of eye. Maxilla concealed by lacrimal when mouth closed, posterior margin of maxilla almost extending to posterior margin of lacrimal. Each jaw with tiny conical teeth, interspace between teeth broader than length of teeth; no vomerine and palatine teeth.

Anterior margin of tongue rounded. Basibranchial with no tooth anteriorly, patches of sharp villiform teeth medially posteriorly. Gill rakers slender, thin laterally, long, visible from side when mouth open. Posterior margins of preopercle and opercle smooth, corner of each broadly rounded. Caudal peduncle low. Both small keels on caudal-fin base converging slightly posteriorly.

Fins. Dorsal fin with VIII–X (usually IX; X in neotype) spines and 11–14 (12 in neotype; usually 12) soft rays followed by 5 (rarely 6) finlets; anal-fin with one rudimentary spine and 8–12 (usually 11, 11 in neotype) soft rays followed by 5 (rarely 6) finlets; pectoral fin with 17–21 (19 in neotype) rays; pelvic fin with I spine and 5 soft rays. First and second dorsal fins widely separated; base of first dorsal fin longer than base of second dorsal fin. First dorsal fin higher than second dorsal fin, second spine longest. First dorsal-fin origin behind vertical through pectoral-fin base. Second dorsal-fin origin one or few rays in advance of origin of anal fin. Soft rays of second dorsal fin progressively shorter from second to seventh ray, remaining rays subequal in length. Length of anal-fin base subequal to base of second dorsal fin. Pectoral fin semitriangular, short, extending past vertical through middle of first dorsal-fin base. Pelvic fin slightly shorter than pectoral fin; origin of pelvic fin between vertical below origins of pectoral and first dorsal fins. Caudal fin forked, shorter than head.

Scales. Body with small finely ctenoid scales, except for larger cycloid scales on nape and in area below pectoral-fin base. Several transverse rows of scales on breast at angle of opercle slanting backwards, becoming vertical from above origin of pelvic fin. Scales between lateral line and origin of first dorsal fin 7.5–10.5 (10.5 in neotype) except for rudimentary scales at base of dorsal fin. Predorsal scales nearly reaching to vertical through posterior edge of eye, ending in deep W shape. Lateral line straight, simple. Head naked except for 3–7 (6 in neotype) rows of thin embedded cycloid scales on preopercle. Second dorsal and anal fins and basal part of pectoral fin scaled, other fins unscaled.

Color when fresh and alive (Figures 11 and 12). Grayish to greenish blue dorsally, silver ventrally, with 2–4 longitudinal rows of black spots above lateral line, its size smaller than half of pupil diameter, lower 1–2 rows sometimes forming simple continuous longitudinal lines. One or two narrow golden longitudinal stripes usually below longitudinal rows of black spots. Black spot on side of body behind pectoral fin, its size somewhat larger than those on dorsum. Black spot at upper pectoral-fin base. Dorsal and pectoral fins dusky, margins darker. Anal and pelvic fins white. Caudal fin dusky or dusky yellow, with black margin. All fins except for caudal fin semitranslucent.

Color in preservation (Figure 10). Body and head dark blue to dark gray dorsally, yellowish brown to yellowish white ventrally. Longitudinal spots or lines and black spot behind pectoral fin when fresh sometimes remain darker than surrounding area (not visible in neotype). Posteroventral margin of preopercle striated. All fins yellowish brown to yellowish white.

Distribution and habitat. The most widespread species of the genus, known in the Indian Ocean from South Africa and the east coast of Africa northward to the Persian/Arabian Gulf, Iran, Pakistan, and India, east through Indonesia, Papua New Guinea, and Marshall Islands to Samoa Islands and Tonga in the Pacific, extending north to southern Japan, south to Australia (Queensland), but absent in the Red Sea where it is replaced by *R. chrysozonus* and possibly the western part of the Gulf of Aden (see Distribution of *R. chrysozonus*).

Epipelagic in coastal areas. Forms small to large schools. Juveniles feed on phytoplankton and small zooplankton, while adults feed on macrozooplankton, mainly larval fishes and shrimps. The intestine becomes relatively shorter with growth, probably reflecting a shift in trophic level due to a transition to a diet consisting entirely of zooplankton) [2].

Remarks. Cuvier (1816) [4] originally named *Scomber kanagurta* in a footnote under *Scomber* without a morphological description, citing plate 136 of Russell (1803) [5] (Figure 13). The latter illustrated a specimen from Vishakhapatnam, India, on the coast of the Bay of Bengal, with a brief morphological description. This description included meristics without value ranges, indicating that the description was based only on a single specimen. Therefore, the specimen illustrated in pl.136 of Russell (1803) [5] is the holotype of *Scomber kanagurta* Cuvier, 1816 by monotypy (ICZN Art. 73.1.2). Russell's (1803) [5] brief description of the holotype, including general body shape, number of fin rays, and coloration, is equivocal with respect to the specimens herein described as *R. kanagurta* and *R. brachysoma*, both currently known from the type locality of *S. kanagurta*. However, the holotype's body depth (body depth 2 as presently referred to) is estimated as ca. 28% of FL, based on plate 136 of Russell (1803) [5]. The total body length of the holotype is reported as 10 inches therein, equivalent to ca. 220–230 mm FL.

The holotype of *S. kanagurta* is conspecific with the present specimens of *R. kanagurta* because the estimated body depth of 28% of FL closely matches that of the latter specimens of similar size (Figure 4; Table 1). Meanwhile, the holotype of *S. kanagurta* and the present specimens of *R. brachysoma* cannot be directly compared, since the latter consists of smaller (<190 mm FL) specimens. Nevertheless, a specimen of *R. brachysoma* is expected to attain much greater body depth than the holotype of *S. kanagurta* at a similar size, as the body becomes deeper with growth (Figure 4). Therefore, we consider that the holotype of *S. kanagurta* more closely resembles the present specimens of *R. kanagurta* than *R. brachysoma*. To avoid further taxonomic confusion, CAS 248440 (previously included in CAS-SU 14594) is designated herein as the neotype of *R. kanagurta* (Figure 10A; Table 2). It was collected from Kozhikode, Kerala, India, near the original type locality, by Albert W. Herre in 1941.

Fricke (1999) [101] designated the specimen illustrated in pl. 136 of Russell (1803) [5] as the lectotype of *Scomber kanagurta* Cuvier, 1816, although the specimen no longer existed [43]. As discussed above, this specimen is the holotype of the species; therefore, Fricke's (1999) [101] designation of the lectotype is invalid.

Cuvier (1829) [84] noted the name "*Scomber canagurta*", which differs from *S. kanagurta* Cuvier, 1816, by only one letter, with an "N" in the footnote on p. 197. However, the footnote merely quoted pl. 136 in Russell (1803) [5], which also served as the basis for *S. kanagurta* Cuvier, 1816, and included no description. Cuvier (1832; p. 49) [59] also referred to "*Scomber kanagurta*, nob", citing Russell (1803) [84]. Thus, Cuvier (1829, 1832) [84] are not considered to have intended to describe a new species. "*Scomber canagurta*" Cuvier (1829) [84] is herein considered an incorrect subsequent spelling and therefore an unavailable name (ICZN Art. 33.3).

Cuvier (1832) [59] not only cited Russell (1803) [5] but also described five specimens of the genus *Rastrelliger* collected from the coasts of India and the Red Sea. Among these, a specimen from the Red Sea is considered to be *S. chrysozonus* redescribed in this study. Bauchot and Branc (1961) [62] regarded these five specimens as syntypes of "*Scomber kanagurta* Cuvier, 1832". However, as noted above, Cuvier (1832) [59] apparently did not intend to describe a new species; thus, these specimens are not considered type specimens.

Several nominal species from various localities have been synonymized under *S. kanagurta*, viz., *Scomber chrysozonus* Rüppell, 1836 (type locality: Red Sea), *Scomber delphinalis* Cuvier, 1832 (Madagascar), *Scomber lepturus* Agassiz, 1874 (unknown locality), *Scomber loo* Lesson, 1829 (New Ireland), *Scomber microlepidotus*, Rüppell, 1836 (Red Sea), *Scomber moluccensis* Bleeker, 1856 (Ambon, Indonesia), *Scomber reani* Day, 1871 (Andaman Islands), *Rastrelliger serventyi* Whitley, 1941 (Western Australia), and *Scomber uam* Montrouzier, 1857 (Woodlark Island, Papua New Guinea) [1,2,43]. Recently, Muto et al. (2016) [18] confirmed the synonymy of species with available types, based on the comparisons with non-types of *R. kanagurta* from the Philippines. These include *S. chrysozonus*, *S. microlepidotus*, *S. moluccensis*, *S. loo*, *S. reani*, and *R. serventyi*. However, we herein redescribed *Scomber chrysozonus* as valid, synonymizing *S. microlepidotus* under it (see above). Regarding the remaining nominal species for which types are available, we consider that they are all synonyms of *R. kanagurta*, being morphologically indistinguishable from the specimens identified here as *R. kanagurta* (Tables 1 and 2). Although Cuvier (1832) [59] also described a nominal species "*Scomber loo*" as "nob.", he referred to Lesson (1829) [85], the original author of the species. Therefore, Cuvier (1832) [59] is not considered to have intended to describe a new species.

Scomber delphinalis is also regarded as a junior synonym of *S. kanagurta*, although no type is known for the former. *Scomber delphinalis* was originally described from Madagascar by Cuvier in Cuvier and Valenciennes (1832) [59], as a mackerel possessing numerous black spots on the back. This feature is shared among all members of *Rastrelliger* as currently recognized, with *R. kanagurta* being the only species occurring in Madagascar. Although Cuvier (1832) [59] showed the author of the nominal species as P. Commerson, Commerson's manuscript was never published, as Cuvier (1832) [59] pointed out. Therefore, the author of the nominal species should be Cuvier (1832) [59]. *Scomber lepturus* was originally named by Agassiz (1874) [88] based on a plate with no accompanying morphological description. Collette & Nauen (1983) [2] and Collette (2003) [43] listed the species as a junior synonym of *R. kanagurta* with no explanation, followed by Fricke et al. (2024) [77]. We also tentatively follow these authors, as the original description was not available to us. *Scomber uam* was originally described from Woodlark Island in the Solomon Sea by Montrouzier (1857) [145]. Collette (2003) [43] listed the nominal species as a junior synonym of *R. kanagurta* with no explanation, followed by Fricke et al. (2024) [77]. However, Montrouzier (1857) [145] originally characterized the species as having 5 dorsal and anal finlets, no swim bladder, and no bands or spots on the back, the features not attributable to members of *Rastrelliger*. *Scomber scombrus* Linnaeus, 1758 is the only known species with the same number of finlets and lacking a swim bladder, but it displays conspicuous wave-like dark bands on the back and is restricted to the Atlantic [2,3]. Because *S. uam* lacks type specimens, its identity with known species cannot be discussed any further. Therefore, *S. uam* is herein regarded as *nomen dubium*.

4. Key to the Species of *Rastrelliger*

1a First dorsal fin usually with X spines; gill rakers short, not visible from side when mouth open, total gill rakers on first gill arch 32–38; maxilla short, extending about three-fourth of lacrimal length; mouth relatively small, upper-jaw length 38.4–44.9% of head length; body slender, distance between origins of first dorsal and pelvic fins (body depth 2) usually less than 22.0% of FL. . .*R. faughni* (northern Indian–western Pacific)

1b First dorsal fin usually with IX spines; gill rakers long, visible from side when mouth open, total gill rakers on first gill arch 47–64; maxilla long, extending almost to hind margin of lacrimal; mouth relatively large, upper-jaw length 42.8–63.8% of head length; body deep to moderately deep, body depth 2 usually more than 22.0% of FL in adults. 2

2a Intestine 3.2–3.6 times longer than FL; body deep, its depth 24.2–28.3% of FL; caudal peduncle relatively deep, its depth 3.8–4.3% of FL; no longitudinal narrow stripe below longitudinal rows of black spots on dorsum. . .*R. brachysoma* (northern Indian–western Pacific)

2b Intestine 1.4–1.8 times longer than FL; body moderately deep, its depth 19.5–25.1% of FL; caudal peduncle relatively slender, its depth 3.0–4.1% of FL; golden to dark longitudinal narrow stripes usually below longitudinal rows of black spots on dorsum. 3

3a Upper-jaw length 54.4–60.0% of head length; distances from snout to base of pectoral fin 28.2–31.4% of FL, to base of pelvic fin 33.1–36.5% of FL; body width 12.4–14.8% of FL. . . . . *R. chrysozonus* (Red Sea)

3b Upper-jaw length 42.8–57.5% of head length; distances from snout to base of pectoral fin 26.4–30.3% of FL, to base of pelvic fin 30.6–35.9% of FL; body width 10.6–14.7% of FL. . . . . *R. kanagurta* (Indo-West Pacific except for the Red Sea)

5. Discussion

We demonstrated that *R. chrysozonus* and *R. kanagurta* maintain distinct gene pools, as indicated by well divergent and reciprocally monophyletic mtDNA clades in the presented phylogeny (Figure 1). This finding supports the conclusion that they are separate species. After the redescription of *R. chrysozonus*, the family Scombridae comprises 55 valid species in 15 genera, including recently described *Scomber indicus* Abdussamad, Sukumaran and Ratheesh, 2016 and *Scomberomorus avirostrus* Abdussamad and Toji, 2023.

Rastrelliger chrysozonus is endemic to the Red Sea and possibly to the western Gulf of Aden, whereas *R. kanagurta* is widespread across the Indo-West Pacific excluding the area occupied by *R. chrysozonus*. These distribution patterns suggest that the historical isolation of the Red Sea drove the initial divergence of the two sibling species. The narrow and shallow Strait of Bab-al-Mandeb, which now connects the Red Sea with the Western Indian Ocean, restricted water exchange between the two regions during the Pleistocene glacial maxima. This process is thought to have limited dispersal and migration of marine organisms, leading to the formation of endemic species or unique populations in the Red Sea that are genetically distinct from their counterparts elsewhere in the Indo-Pacific (reviewed in [146–148]). Estimating the divergence time for *R. chrysozonus* and *R. kanagurta* would help to associate their separation with such historical process with more confidence.

The current maintenance of distinct, non-overlapping distribution ranges for *R. chrysozonus* and *R. kanagurta* is an intriguing question. The apparent lack of a physical barrier to dispersal/migration and the potentially high mobility of these species might facilitate range extensions. Their non-overlapping distributions despite such features may be attributed to the mutual exclusion of ecologically similar species and the unique environment of the Red Sea. The modern Red Sea is characterized by extremely high salinity, occasionally exceeding 40 ppt, due to minimal input of freshwater and a high evaporation rate [149]. Salinity levels were even higher during the Pleistocene glacial maxima due to reduced water exchange with the Western Indian Ocean [150]. Such harsh environmental conditions may have been preventing the immigration of *R. kanagurta*. In addition, adaptation of *R. chrysozonus* to the Red Sea environment may have been enhancing its success in this habitat while reducing its fitness elsewhere as a tradeoff, restricting its distribution [151].

The lack of a single diagnostic character distinguishing *R. chrysozonus* from *R. kanagurta* complicates their identification. Although the two species differ in some measurements, they show considerable overlaps in these characters, with each species exhibiting allometric changes (Figure 4; Tables 1 and 3). Preferably, specimen identification is based on a combination of morphology and genetics, complemented by the specimen's locality of origin. Fisheries management and conservation efforts, which rely on accurate species identification, should fully acknowledge this difficulty.

Our phylogenetic analysis demonstrated clear interspecific divergence among the three species of *Rastrelliger* occurring in the Indian and Pacific Oceans with estimates of K2P distance of 0.03 between *R. kanagurta* and *R. chrysozonus*, corroborating previous studies [18,51,56]. While a previous study speculated that the intraspecific divergence they observed in *R. kanagurta* might warrant subspecies status [51], others attributed this intraspecific divergence to historical vicariance followed by range expansion, potentially driven by geological and oceanographic processes [18,56]. They called for more thorough analysis using nuclear markers to better understand the evolutionary processes underlying the observed divergence.

The taxonomic status of a group of organisms can affect its conservation and management [152]. Recent genetic studies indicate that widely distributed pelagic marine fishes, once considered single panmictic entities, are often subdivided into distinct lineages or populations (e.g., [153–155]). However, the taxonomic status of such lineages or populations often remains unresolved, potentially undermining their management. The present study illustrates how molecular phylogenetic analysis within an integrative taxonomic framework can lead to a revised taxonomy of marine fishes.

The resurrection of *R. chrysozonus* aligns with growing evidence for a much higher number of endemic species in the Red Sea than previously estimated. Integrative taxonomic approaches have also led to the description or redescription of endemic Red Sea species across various fish groups (e.g., [156,157]).

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17010072/s1, Figure S1, The illustration of morphometric characters examined in the present study. Table S1, The list of the specimens examined. References [158–165] are cited in the Supplementary Materials.

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