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Contributions to the Taxonomy of the Mugilid Genus *Moolgarda* Whitley (Teleostei: Mugilidae), with Redescriptions of *M. crenilabis*, *M. seheli* and *M. tade* from the Red Sea

Sergey V. Bogorodsky [1,2,*], Philipp Thieme [3,4], Hiroshi Senou [5], Zuheir N. Mahmoud [6], Tilman J. Alpermann [2] and Jean-Dominique Durand [4]

1 Station of Naturalists, Omsk 644089, Russia
2 Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; tilman.alpermann@senckenberg.de
3 Deutsches Meeresmuseum, Katherinenberg 14-20, 18439 Stralsund, Germany; phil.thieme2016@gmail.com
4 MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, 34095 Montpellier, France; jean-dominique.durand@ird.fr
5 Kanagawa Prefectural Museum of Natural History, 499 Iryuda, Odawara 350-0031, Japan; senou@nh.kanagawa-museum.jp
6 Department of Zoology, Faculty of Science, University of Khartoum, Khartoum 11115, Sudan; zuheirnm@hotmail.com
* Correspondence: ic187196@yandex.ru

Abstract: The taxonomy of the family Mugilidae has historically posed challenges, marked by discrepancies between described and valid species, compounded by cryptic diversity and a similar external appearance. Previous studies left four of six lineages unidentified within *Crenimugil*, including *Crenimugil* sp. A and *Crenimugil* sp. B. The goal of this study is to provide a detailed revision of species assigned to *Crenimugil* by examining specimens from the Red Sea, which is the type locality of *Mugil crenilabis*, *Mugil seheli* and *Mugil tade*, which were here genetically analyzed. After demonstrating that the genus contains nine monophyletic lineages and *Moolgarda pura* is a valid nominal species, the mugilid genus *Moolgarda* is restored. Consequently, *Moolgarda* has priority over *Crenimugil* and *Valamugil*. Additional morphological analyses of specimens from the Red Sea assigned to *Moolgarda* sp. A and *Moolgarda* sp. B identified them as representing *Moolgarda seheli* and *Moolgarda crenilabis*, respectively. A phylogenetic analysis, including new DNA barcodes, confirmed a wide distribution range of both species in the Indo-West Pacific. The identity of the lineage previously identified as *Crenimugil crenilabis* remains doubtful, and it is referred to as *Moolgarda* cf. *crenilabis* here. A third lineage, previously named *Crenimugil buchanani*, is re-described as *Moolgarda tade*, a species originally reported from the Red Sea with a long history of taxonomic confusion. The species is widely distributed in the Indo-West Pacific and distinguished from other congeners by falcate second dorsal and anal fins that are distinctly higher than the first dorsal fin. A detailed description of the Red Sea specimens of *M. crenilabis*, *M. seheli* and *M. tade* is provided, with comments to other unnamed lineages.

Keywords: mugiliformes; Rhinomugilinae; *Crenimugil*; phylogenetic analysis; Indo-West Pacific; distribution

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1. Introduction

Recent studies on the molecular phylogeny of the family Mugilidae Jarocki, 1822 have provided improved knowledge about the systematic relationships of species of different mugilid genera, which previously was a matter of confusion [1–6]. Xia et al. in 2016 [4] recognized four subfamilies (Myxinae, Mugilinae, Rhinomugilinae and Cheloninae) based on a comprehensive and integrative analysis of morphological and genetic characters. The subfamily Rhinomugilinae comprises eleven genera, including *Crenimugil* Schultz, 1946. In their phylogenetic analysis, based on nucleotide variation from 3 mitochondrial genes

(Cytochrome Oxidase subunit 1 (COI), 16S RNA and Cytochrome b (*cytb*)), Durand and Borsa [3] recognised six genetic lineages within *Crenimugil*: *C. buchanani* (Bleeker, 1853), *C. crenilabis* (Forsskål, 1775), *C.* sp. A, *C.* sp. B., *C.* sp. C and *C.* sp. D.

In the Red Sea, two valid species belonging to the genus *Crenimugil* Schultz, 1946 have been described, namely *C. crenilabis* and *C. seheli* (Fabricius, 1775) (e.g., [7]). Both species are common in that area and of commercial interest. Originally, both species were described in the genus *Mugil*, and later, *Mugil crenilabis* was recognised in the genus *Crenimugil*, whereas *Mugil seheli* was recognised in the genus *Moolgarda* Whitley, 1945 [8]. When both species were shown to be part of the same phylogenetic clade [1,3,4], the genus name *Crenimugil* was retained [1]. Although the genus name *Moolgarda* predates that of *Crenimugil*, Durand et al. [1] followed Thomson [9], who considered *Moolgarda* a nomen dubium since the type specimen of *Moolgarda pura* Whitley, 1945, the type species of *Moolgarda*, has been lost. However, the presence of the type specimen of *M. pura* is still debated, and illustrations and data presented in the original description indicate that the holotype may has been mixed with specimens of a different species [10,11]. Based on the depictions provided in Whitley [10], Kottelat [11] inferred that *M. pura* possibly represents either *C. buchanani* or *C. seheli*. Therefore, the validity of the genus name *Crenimugil* remains doubtful. Furthermore, it is currently not known which of the species defined by Durand and Borsa [3] refers to *C. seheli*. Specimens identified as *C. seheli* based on morphological characters were present in every unnamed *Crenimugil* lineage in an analysis conducted by Durand et al. [12], suggesting that by default a specimen from the genus *Crenimugil* is recognised as *C. seheli*.

In genetic analyses so far, the genus *Crenimugil* was only studied based on material from the Indian and western Pacific Ocean. However, both *C. crenilabis* and *C. seheli* were first described from the Red Sea. Furthermore, two more species were described from the Red Sea, *Mugil crenilabis our* Fabricius, 1775 and *Mugil crenilabis tade* Fabricius, 1775. While the former species may be recognized as a valid species currently placed in synonymy with *Mugil cephalus* Linnaeus 1758, the latter is placed in the genus *Planiliza* as a valid species without explanation (see [8]).

In this study, we discuss the using of the genus name *Crenimugil* and the controversy of the holotype of *Moolgarda pura*. For the first time, we analysed specimens of the genus *Crenimugil* from the Red Sea, type locality of *C. crenilabis*, *C. seheli* and *C. tade*. In order to potentially assign *C. seheli* to one of the unnamed genetic lineages described in Durand and Borsa [3], we compared morphological characters for positive identification of *C. seheli* and sequenced mitochondrial and nuclear markers. We further present valuable data for the presence of two other genetic lineages in the Red Sea corresponding to the species first described by Forsskål and Fabricius.

2. Material and Methods

2.1. Sampling

A total of 57 specimens from the Red Sea and adjacent regions (Socotra, Yemen, Oman, Iran) were sampled and sequenced in this study. An additional 285 specimens identified as *Crenimugil* spp. from the Indo-Pacific were also DNA barcoded to further investigate the genetic diversity of the genus and spatial distribution range of the different lineages (Bold data set DS-MOOLG). A fin clip or piece of muscle from dorsal part of body from each specimen were taken and stored in a 1.5 mL Eppendorf tube with 90–96% ethanol and later stored at −20 °C.

2.2. Laboratory Protocol

Total genomic DNA was extracted from ethanol-preserved tissues using Pure Link DNA Extraction kit following the companies' recommendations, Thermo Fisher Scientific (Waltham, MA, USA), Invitrogen PureLink™ Genomic DNA Mini Kit. All specimens were first DNA barcoded using the cytochrome oxydase 1 (COI) marker using primers FishF1 + FishF2/FishR1 [13]. Polymerase chain reaction (PCR) was conducted in a total volume of 40 µL containing 20 µL of DreamTaq PCR Hot Start Mastermix (Thermo Fisher

Scientific), 16 µL of ultrapure water, 0.8 µL of BSA (Euromedex, Souffelweyersheim, France), 0.6 µL of reverse and forward primers (0.15 µM) and 2 µL of DNA template. The conditions used during PCR reaction were as follows: initial denaturation temperature at 92 °C for 5 min followed by 35 cycles of strand denaturation at 92 °C for 1 min, primer annealing at 52 °C for 45 s, primer extension at 72 °C for 90 s and a final extension at 72 °C for 5 min. Sanger sequencing of both strands was performed by Genoscreen (Lille, France) with the same primers used in PCR amplification. DNA sequences were edited, aligned using MEGA 7.0.26 [14]. All COI sequences have been uploaded in BOLD to obtain the barcode index number (BIN) that correspond to molecular operational taxonomical unit (MOTU). Secondly, for some representative specimens of the different BINs, portions of two mitochondrial genes (16SRNA and cytochrome b: *Cytb*) and three nuclear loci (*RAG*, *Enc-1*, *Myh6*) were amplified by PCR or nested PCR using the primers from published works [1,4]. Resulting PCR products were Sanger sequenced with the same primers used in amplification reactions. The list of primes is included in the Supplementary Table S2.

2.3. Phylogenetic Analyses

Phylogenetic relationships among species of the genus *Moolgarda* were investigated using two datasets: (1) All new COI barcodes obtained in this study (DS-MOOLG, 342 specimens) plus all available DNA barcodes from BOLD (consultation on 24 April 2023) belonging to BINs assigned to the genus *Moolgarda* (166 specimens) (Supplementary Table S1, associated with Figure 1). (2) A concatenated alignment of the three mitochondrial fragments (2041 base pairs) plus three nuclear fragments (2695 base pairs) were obtained for a limited subset of individuals, representing the different evolutionary lineages highlighted in the COI tree (dataset 1). Kimura 2-parameter distances among COI DNA barcodes of the genus '*Crenimugil*' were estimated using MEGA 7.0.26 [14] and genetic similarities among specimens were depicted in a neighbour joining tree (NJ [15]). Phylogenetic analyses of the second (multi-marker) dataset were conducted based on a partitioned maximum-likelihood (ML) method as implemented in IQ-TREE [16]. The partitions were set by gene, and the best substitution model was identified using ModelFinder [17]. The best-fit model according to Bayesian information criterion scores was TIM2e + G4 for the 16SRNA section, HKY + F + G4 for the COI section, TIM2 + F + I + G4 for the *Cytb* section, K2P + I for the *RAG* section, K3P + I for the *Enc-1* section and TN + F + I for the *Myh6* section. Nodal support was assessed with Ultrafast bootstrapping Hoang et al. [18] based on 1000 pseudo-replicates. The ML analysis was conducted with the IQ-Tree web server [19]. The phylogenetic trees were visualized and edited under FigTree v1.4.0. Homologous sequences of *Osteomugil robustus* and *O. perusii* were chosen as outgroups to root the reconstructed phylogenetic trees (see Figure 1).

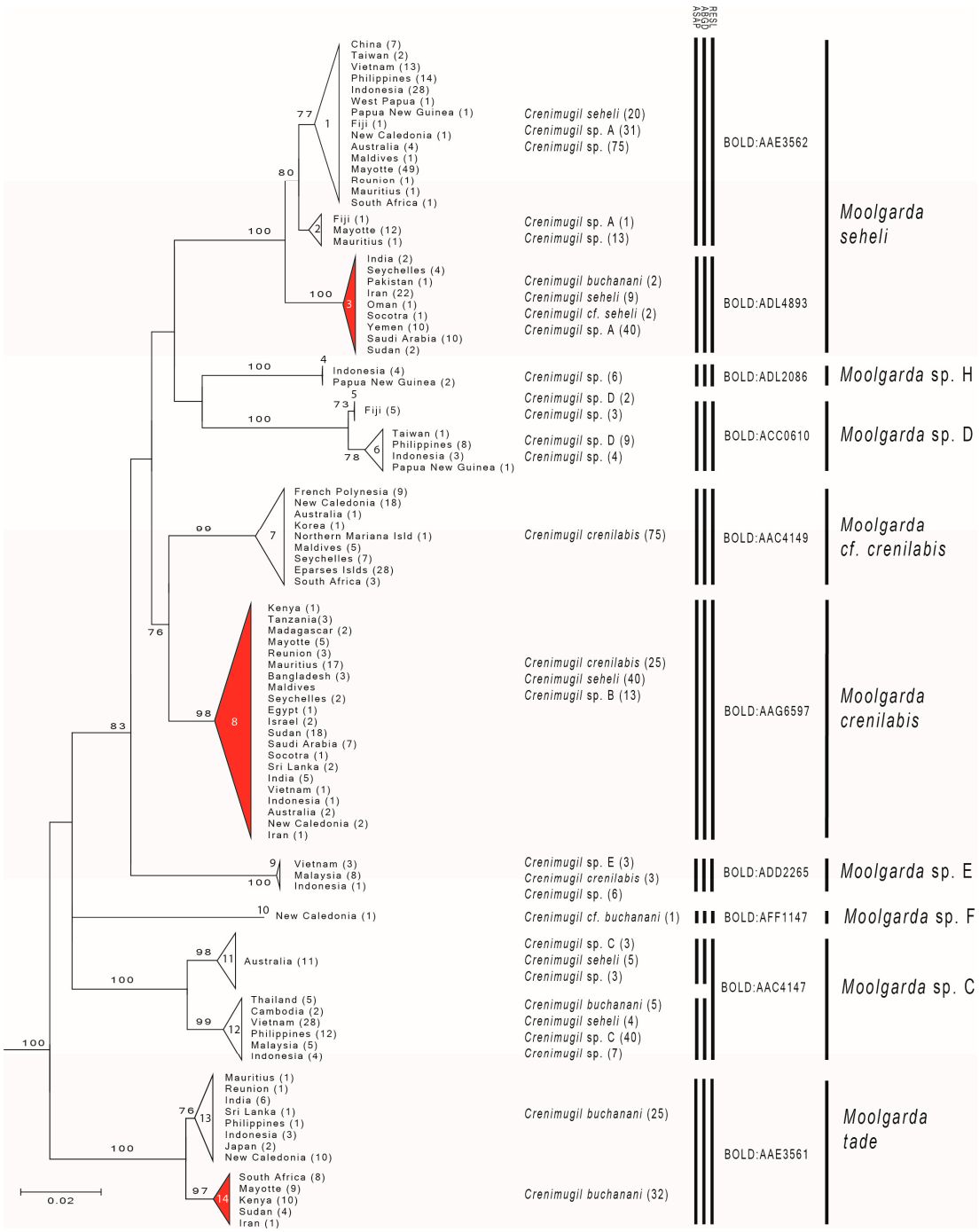

Figure 1. Phylogenetic relationships among specimens belonging to the genus *Moolgarda* inferred by the maximum-likelihood analyses with HKY + F + G4 nucleotide substitution model based on COI barcodes dataset (Supplementary Table S1). Branch length is proportional to inferred number of nucleotide substitutions. The tree was rooted with *Osteomugil robustus* and *O. perusi*. Numbers at nodes represent bootstrap values in percentages. Bootstrap values < 70% are not shown. Numbered triangles on tips of the tree represent lineages and sublineages for which members are listed in Supplementary Table S1. The height of the triangle is proportional to the genetic diversity recovered among members of the clade. For each lineage and sublineage, geographic origin, species name and effective are mentioned on the right. Red triangle are clades observed in the Red Sea. Results from species delimitation analyses based on COI gene sequences using the ASAP, ABGD and RESL algorithms, as well as species name identified for each evolutionary lineage, are mentioned on the right of the tree.

2.4. Species Delimitation Analyses

The COI barcode dataset (Supplementary Table S1) was analyzed for the purpose of delimiting species. The analysis focused solely on the COI barcode dataset, as Durand et al. [12] demonstrated for the Mugilidae family that this marker successfully recovered all known and presumed cryptic species flagged previously using concatenation of three different markers [3]. Furthermore, due to its widespread use in taxonomic studies and DNA barcoding projects, a large amount of genetic data using COI is available in the Barcode of Life Data Systems (BOLD). Three different DNA-based approaches were used: the automatic barcode gap discovery (ABGD) algorithm [20], the refined single linkage (RESL) as implemented in BOLD and used to produce barcode index numbers (BINs [21]) and the assemble species by automatic partitioning (ASAP) method [22]. All approaches cluster nucleotide sequences into MOTUs or putative species without a priori species hypotheses. The ABGD and ASAP algorithm analyses were conducted using the online version of ABGD http://wwwabi.snv.jussieu.fr/public/abgd/ (accessed on 25 April 2023) and ASAP https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html (accessed on 25 April 2023) with the K2P [23] and Jukes-Cantor (JC69) [24] pairwise distance models; other parameters were set as default.

2.5. Morphological Analyses

Eleven Red Sea specimens from the collection of the Senckenberg Research Institute and Natural History Museum in Frankfurt (SMF) and the King Abdulaziz University Marine Museum (KAUMM) in Jeddah as well as 12 out of 24 specimens from the Red Sea, Sudan were examined. Further, one specimen from the type locality of *Moolgarda pura* from the Australian Museum in Sydney was examined (AMS-IB.1568) as well as the type specimen of *Mugil fasciatus* (type locality Red Sea) stored at the Museum National d'Histoire naturelle (MNHN) in Paris. Morphometric measurements were conducted using a digital calliper to the nearest 0.1 mm. Measurements and meristic data were taken from all specimens following Thieme et al. [5]. The last two rays of the second dorsal fin were counted as two separate rays following [25].

3. Results

3.1. Reviving the Genus Moolgarda

Schultz [26] created a new genus *Crenimugil* for *Mugil crenilabis* characterised by having a thick upper lip bearing papillae and a lower lip with a crenulated edge. One year earlier, Whitley [10] had described a new genus, *Moolgarda*, and a new species, *M. pura*, based on a single specimen but without holotype registration. Thomson [9] argued that the description of *M. pura* was based on two species of different genera, one of them *Liza subviridis* (Valenciennes, 1836), that lacks a pectoral axillary scale. Further, he stated that the holotype of *M. pura* is lost and only other specimens included in Whitley's description were found in the collection of the Australian Museum [9]. Therefore, he considered the species a nomen nudum and a nomen dubium. Durand et al. [1] followed Thomson [9] and treated *Crenimugil* as a valid genus and placed *Valamugil* Smith, 1948 (type species *M. seheli*) in its synonymy. However, Whitley ([10], p. 16, Figure 8) clearly wrote that his description and figure were based only on one female specimen (holotype) of 490 mm TL from Point Cloates, Western Australia, validating the name *Moolgarda pura*.

While Senou (in [27], p. 1511) noted that *Moolgarda pura* is 'undoubtedly the same species as *Mugil seheli*', Kottelat [11] raised some doubt and suggested that *M. pura* potentially is a synonym of *M. buchanani*. While he refers to the identification key provided by Harrison & Senou [28], *M. seheli* and *M. buchanani* can be distinguished by their morphology. We analysed a specimen identified as *M. seheli* (AMS IB.1568) from the type locality of *Moolgarda pura* that fits the description provided by Whitley [10]. Therefore, *M. pura* is a junior synonym of *M. seheli*. Hence, the genus name *Moolgarda*, which predates that of *Crenimugil*, should be retained [1,4]. Subsequently, *Mugil crenilabis* is to be recognised as *Moolgarda crenilabis* and *Crenimugil* becomes a junior synonym of *Moolgarda*. Because

Valamugil, which was described by Smith [29], is also based on *Mugil seheli*, the genus is a junior synonym of *Moolgarda* too. A specimen from the collection of the Museum and Art Gallery of the Northern Territory is planned to be designated as neotype for *Moolgarda pura* (Ghasemzadeh and Hoese, personal communication).

The phylogeny provided by Xia et al. [4] supports the division of the subfamily Rhinomugilinae into four tribes: Trachystomaini, Rhinomugilini, Squalomugilini and Crenimugilini. They provided morphological and osteological characters to distinguish genera of the family. The tribe Crenimugilini contains two genera, *Moolgarda* and *Osteomugil*. While these two genera were classified as a single genus *Moolgarda* by Ghasemzadeh [30], they are clearly distinguishable genetically as well as morphologically by the position of the second dorsal fin in relation to the anal fin, development of adipose tissue around eye, and two osteological characters [4]. Species of *Osteomugil* possess the second dorsal-fin origin below the anterior third of the anal fin and the adipose tissue on the eye is well developed, whereas the second dorsal fin origin opposite or slightly posterior to the anal fin origin and the adipose tissue has a narrow rim around the eye in *Moolgarda*. Two species of the tribe Squalomugilini, *Ellochelon vaigiensis* (Quoy & Gaimard, 1825) and *Plicomugil labiosus* (Valenciennes, 1836), also distributed in the Red Sea, easily differ from *Moolgarda. Ellochelon vaigiensis* can be distinguished by its having 8 anal-fin rays, a caudal fin which is slightly emarginate to truncate, finely ctenoid scales with 25–29 rows in longitudinal series and 26–48 pyloric caeca rather than an anal fin with 9–10 rays, forked caudal fin, cycloid scales with a membranous edge, 33–42 scales in longitudinal series and 6–10 pyloric caeca in *Moolgarda*. *Plicomugil labiosus* differs with its very thick upper lip with a deep fold near its ventral edge, splitting it into upper and lower lobes, fringed with small ridges of horny epidermal tissue, finely ctenoid scales, deeply notched preorbital, maxilla exposed posteriorly when mouth is closed and 3 pyloric caeca versus upper lip when thick is not divided into lobes, scales cycloid with membranous edge, preorbital weakly concave, maxilla concealed posteriorly by preorbital when mouth is closed and 6–10 pyloric caeca in *Moolgarda*.

The species of the genus *Moolgarda* possess the following characters which preliminary may bear diagnostic value: anal-fin rays 9–10 (usually 10); scales cycloid, with crenulate membranous edge; preorbital weakly concave on serrated anteroventral edge, not kinked, posterior end obtuse; posterior end of maxilla concealed by preorbital when mouth closed; adipose tissue a narrow rim around eye; origin of the second dorsal fin from opposite origin of anal fin to below anterior one-fourth of anal-fin base; pectoral axillary scale well-developed, moderately long; and pyloric caeca 6–10 ([28]; present study).

References are given only for the Red Sea records and previous phylogenetic analysis; also, only the synonymy of the Red Sea nominal species is included.

3.2. Genetic Analyses

Phylogenetic relationship reconstruction of the genus *Moolgarda* using all available COI barcodes yielded nine evolutionary lineages, of which some were formed of sublineages (Figure 1). Red Sea specimens belong to lineage 8 and two sublineages (3 and 14), for which only one (sublineage 14) consists of specimens originally identified by the same species name: *Crenimugil buchanani*. All specimens of this sublineage are from the Western Indian Ocean and the Red Sea, while specimens from the sister-sublineage 13, also originally identified as *C. buchanani*, are from the central Indian Ocean (India) to the South West Pacific (New Caledonia). While reciprocal monophyly of the Indian Ocean and Pacific sublineages is moderately supported, with branch support values of 76% and 97% in bootstrapped analyses of the COI gene, all species delimitation approaches failed to highlight any barcode gaps between them (Figure 1); i.e., they are recognized as one lineage (=species) by these approaches. Lineage 8 containing Red Sea specimens consists of specimens genetically identified as *Crenimugil* sp. B. However, the specimens of this clade from the Red Sea were previously identified as *C. crenilabis* and specimens from the Indian Ocean as *C. seheli* based on their morphology. All three species delimitation approaches used here

support the species status of this lineage. Sublineage 3 forms part of a higher lineage along with two other sublineages (1 and 2). However, sublineage 3, containing the Red Sea and Indian Ocean specimens, is recognized as a separate species by all three delimitation approaches. The other two sublineages form one hypothetical species in all three analyses. Specimens of sublineage 3 containing Red Sea specimens were identified as *Crenimugil* sp. A using genetic identification methods or either *Crenimugil seheli* or *C. buchanani* using morphological approaches. Among these three sublineages, two present barcoding gaps were flagged by all automatic species delimitation methods. More generally, these methods identified the same specimen partitions with one exception, the BIN AAC4147, which is considered two MOTUs according to ASAP and ABGD (Figure 1).

The multi-marker phylogeny is well resolved (Figure 2; Table 1). The three species observed in the Red Sea are the only ones to which a clear species name has been given, while all others are provisionally named following the interim nomenclature proposed by Durand and Borsa [3]. However, several changes are suggested in agreement with present findings (see hereafter). First, the genus name *Crenimugil* is changed to *Moolgarda*. Second, the species name *Crenimugil* sp. B is renamed *M. crenilabis*, while the former *C. crenilabis* is now *M.* cf. *crenilabis*. Further, *Crenimugil* sp. A is renamed *M. seheli*, while *Crenimugil buchanani* (sensu Durand and Borsa [3] is herein renamed *M. tade*. This last species is the most divergent species among all *Moolgarda* species. A sister relationship is stressed between *M. crenilabis* and *M.* cf. *crenilabis*. Last, *Moolgarda seheli* presents close phylogenetic affinities with two undescribed species of the coral triangle: *M.* sp. H and *M.* sp. D (Figure 2).

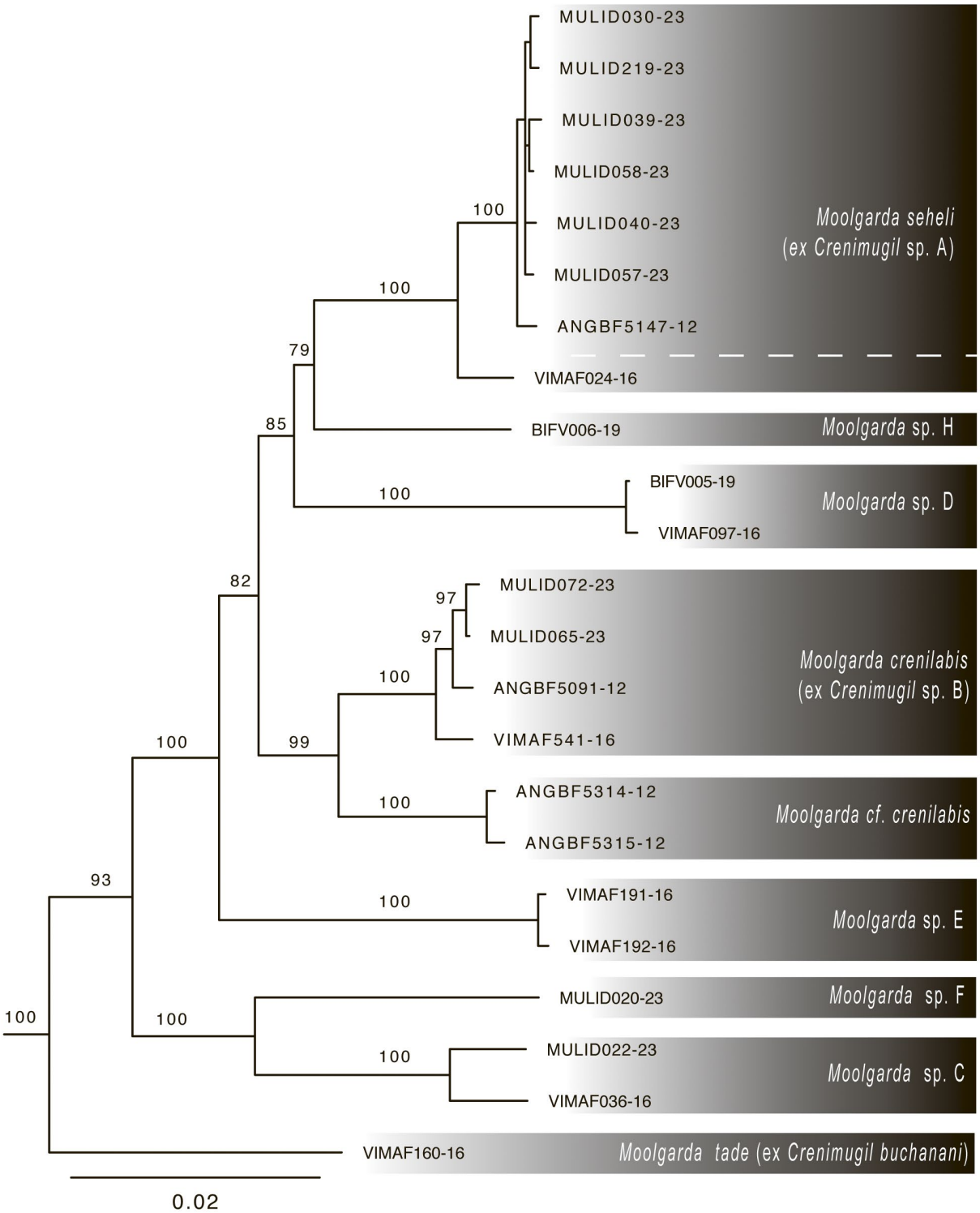

Figure 2. Phylogenetic relationships among species (corresponding to Table 1) belonging to the genus *Moolgarda* inferred by the maximum-likelihood analyses of the partitioned concatenated alignment method with a combination of substitution models (see M&M) specific of portions of three mitochondrial genes (on left) and three portions of nuclear genes (on right). Branch length is proportional to inferred number of nucleotide substitutions. The tree was rooted with *Osteomugil robustus* and *O. perusi*. Numbers at nodes represent bootstrap values in percentages. Bootstrap values < 70% are not shown. Dashed line indicates the BIN distinction previously noticed in the COI phylogenetic tree (Figure 1) between sublineage 3 (BOLD:ADL4893) and sublineages 1 + 2 (BOLD:AAE3562).

Table 1. List of *Moolgarda* specimens used for the multi-marker phylogenetic analysis. Samples arranged following the order given in Figure 2.

Current Species ID (with Photo Marked with *)	In Durand & Borsa 2016 [3]	BOLD Process ID	BIN BOLD:	Sample Identifier	Catalog Museum Number	Locality	COI	16S	*Cytb*	*RAG*	*ENC-1*	*Myh6*
Moolgarda seheli	*Crenimugil* sp. A	MULID030-23	ADL4893	K-14	n/a	Iran, Chabahar Bay	OR923746	OR859515	OR859535	OR859458	OR859476	OR859494
Moolgarda seheli	*Crenimugil* sp. A	MULID219-23	ADL4893	K-15	n/a	Iran, Chabahar Bay	OR923871	OR859523	OR859543	OR859466	OR859483	OR859502
Moolgarda seheli	*Crenimugil* sp. A	MULID039-23	ADL4893	M-1131	n/a	Yemen (Gulf of Aden), Khor Ambekha	OR923941	OR859527	OR859547	n/a	OR859487	OR859506
Moolgarda seheli	*Crenimugil* sp. A	MULID058-23	ADL4893	Sudan-10	n/a	Red Sea, Sudan, Port Sudan	OR923755	OR859517	OR859537	OR859460	OR859478	OR859496
Moolgarda seheli	*Crenimugil* sp. A	MULID040-23	ADL4893	M-1132	n/a	Yemen (Gulf of Aden), Khor Ambekha	OR923923	OR859525	OR859545	OR859468	OR859485	OR859504
Moolgarda seheli	*Crenimugil* sp. A	MULID057-23	ADL4893	Sudan-1	n/a	Red Sea, Sudan, Port Sudan	OR923978	OR859529	OR859549	OR859471	OR859489	OR859508
Moolgarda seheli	*Crenimugil* sp. A	ANGBF5147-12	ADL4893	215	MNHN ICOS-00266	Oman, Ra's al-Hadd	JQ060522	KF375041	KF375120	KF375572	KF375199	KF375352
Moolgarda seheli	*Crenimugil* sp. A	VIMAF024-16	AAE3562	LTV_CH_24	n/a	Cau Hai, Vietnam	OR923810	OR859520	OR859540	OR859463	OR859481	OR859499
Moolgarda sp. H *		BIFV006-19	ADL2086	PNG10	NTUM10007	Papua New Guinea	MT884959	OR859518	OR859538	OR859461	OR859479	OR859497
Moolgarda sp. D *	*Crenimugil* sp. D	BIFV005-19	ACC0610	PNG9	NTUM10006	Papua New Guinea	MT885131	OR859531	OR859551	OR859473	OR859491	OR859510
Moolgarda sp. D	*Crenimugil* sp. D	VIMAF097-16	ACC0610	LTP_NI_06	n/a	Negros Isld, Philippines	OR923956	OR859528	OR859548	OR859470	OR859488	OR859507
Moolgarda crenilabis *	*Crenimugil* sp. B	MULID072-23	AAG6597	Sudan-5	n/a	Red Sea, Sudan, Port Sudan	OR923939	OR859526	OR859546	OR859469	OR859486	OR859505
Moolgarda crenilabis *	*Crenimugil* sp. B	MULID065-23	AAG6597	Sudan-20	n/a	Red Sea, Sudan, Port Sudan	OR923754	OR859516	OR859536	OR859459	OR859477	OR859495
Moolgarda crenilabis	*Crenimugil* sp. B	ANGBF5091-12	AAG6597	221a	n/a	Tanzania, Stone Town, Zanzibar	JQ060634	KF375042	KF375121	KF375573	KF375200	KF375353
Moolgarda crenilabis *	*Crenimugil* sp. B	VIMAF541-16	AAG6597	090316-1	n/a	Con Dao Isld, Vietnam	OR923913	OR859524	OR859544	OR859467	OR859484	OR859503
Moolgarda cf. *crenilabis* *	*Crenimugil crenilabis*	ANGBF5314-12	AAC4149	190	MNHN 2008-1002	French Polynesia, Moorea	JQ060437	KF375040	KF375119	KF375571	KF375198	KF375351
Moolgarda cf. *crenilabis* *	*Crenimugil crenilabis*	ANGBF5315-12	AAC4149	185	MNHN 2009-0808	French Polynesia, Gambier Isl.	JQ060435	JQ060685	KF375173	KF375570	n/a	KF375350
Moolgarda sp. E		VIMAF191-16	ADD2265	TTVT_10_4	n/a	Bai sau, Kien Giang, Vietnam	KT728938	OR859521	OR859541	OR859464	n/a	OR859500
Moolgarda sp. E		VIMAF192-16	ADD2265	TTVT_10_5	n/a	Bai sau, Kien Giang, Vietnam	KT728939	OR859530	OR859550	OR859472	OR859490	OR859509

Table 1. *Cont.*

Current Species ID (with Photo Marked with *)	In Durand & Borsa 2016 [3]	BOLD Process ID	BIN BOLD:	Sample Identifier	Catalog Museum Number	Locality	COI	16S	*Cytb*	*RAG*	*ENC-1*	*Myh6*
Moolgarda sp. F		MULID020-23	AFF1147	VBNCST696	n/a	New Caledonia, Nera estuary	OR923967	KF375043	KF375122	KF375574	KF375201	KF375354
Moolgarda sp. C	*Crenimugil* sp. C	MULID022-23	AAC4147	569a-EP	n/a	beelbi creek, Queensland, Australia	OR924059	OR859533	OR859553	OR859475	OR859493	OR859512
Moolgarda sp. C	*Crenimugil* sp. C	VIMAF036-16	AAC4147	LTV_CH_36	n/a	Cau Hai, Vietnam	OR923858	OR859522	OR859542	OR859465	OR859482	OR859501
Moolgarda tade	*Crenimugil buchanani*	VIMAF160-16	AAE3561	LTP_NI_49	n/a	Negros Island, Philippines	OR923804	OR859519	OR859539	OR859462	OR859480	OR859498
Outgroup												
Osteomugil robustus		MULID021-23	AAG6596	20110628 port3		Reunion Isld, Le port	OR974843	KF375071	KF375149	KF375609	KF375236	KF375387
Osteomugil perusii		MULID096-23	ACC0061	RX12		Taiwan	OR974844	KF375070	KF375148	KF375608	KF375235	KF375386

3.3. Morphological Analyses

***Moolgarda crenilabis* (Forsskål, 1775).**

Fringelip Mullet.

Figures 3 and 4, Table 2.

Mugil crenilabis Forsskål in Niebuhr, 1775 [31], 73 (Red Sea; no types known)—Rüppell 1838 [32], 132 (description); Cuvier & Valenciennes 1836 [33], 123 (description); Klunzinger 1870 [34], 826 (Al Quseir, description); Klunzinger 1884 [35], 132 (Red Sea, description); Fowler 1931 [36], 247 (Sudan); Roux-Estève & Fourmanoir 1955 [37], 196 (Abu Latt, Saudi Arabia, listed); Roux-Estève 1956 [38], 65 (Abu Latt, Saudi Arabia, listed).

Liza crenilabis—Marshall 1952 [39], 242 (Sanafir I., listed).

Crenimugil crenilabis—Klausewitz 1967 [40], 57 (Sarso I., listed); Ben-Tuvia 1975 [41], 17–18 (Nabq, Egypt and Eritrea, key); Dor 1984 [42], 190 (listed); Thomson & Luther 1984 [43] (map, description); Goren & Dor 1994 [44], 51 (listed); Thomson 1997 [9], 505 (description); Khalaf & Disi 1997 [45], 143 (Jordan, description); Khalaf 2004 [46], 43 (Jordan, listed); Golani & Lerner 2007 [47], 257 (listed); Fricke 2008 [48], 20 (nomenclature); Golani & Bogorodsky 2010 [49], 38 (listed); Golani & Fricke 2018 [8], 118 (listed).

Mugil fasciatus Valenciennes in Cuvier & Valenciennes, 1836 [33], 125.

Mugil rueppellii Günther, 1861 [50], 458.

Crenimugil sp. B—Durand & Borsa 2015 [3], 268 (phylogenetic tree).

Diagnosis. Second dorsal-fin rays 9–11; anal-fin rays 9–10; scales cycloid with crenulate membranous edge, 36–40 in longitudinal series; lips toothless; upper lip very thick anteriorly, its lower part with several rows of small papillae, lower lip thin, with a row of papillae forming a fringe; ventral edge of preorbital weakly concave at corner of mouth, posterior end of maxilla concealed when mouth closed; origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin; second dorsal fin subequal in height to first dorsal fin but slightly lower than anal fin; reaches 490 mm SL.

Description. Body moderately elongate, robust, body depth at origin of first dorsal fin 3.4–4.4 in SL and caudal peduncle compressed. Head depth equal to or greater than head width, head length 3.4–4.4 in SL. Snout relatively blunt, slightly shorter than orbit diameter, eye diameter 3.5–4.4 in head length. Interorbital region wide and almost flat, its width more than 1.5 times eye diameter and subequal to postorbital length. First dorsal fin with IV spines, second fin with 9–10 rays. Origin of first dorsal fin midway or closer to base of caudal fin than to tip of snout. Origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin. Second dorsal fin about equal in height to first dorsal fin but slightly lower than anal fin. Anal fin with III spines and 9–10 rays. Outer margin of second dorsal and anal fins emarginate. Pectoral-fin rays 16–18. Tip of pectoral fin not reaching or just reaching a vertical at origin of first dorsal fin and not behind tip of pelvic-fin spine. If laid forward, pectoral fin not reaching anterior edge of eye. Tip of pelvic fin at vertical of origin of first dorsal fin. Caudal fin forked or deeply emarginate. Pyloric caeca 7–10 [30].

Adipose eyelid a narrow rim around eye, adipose tissue covers larger area anterior to eye, reaching posterior nostril. Preorbital fills space between eye and mouth. Preorbital serrated along antero-ventral to the posterior edge starting from above corner of mouth (Figure 3). Ventral edge of preorbital weakly concave, not kinked, at corner of mouth. Posterior end of preorbital obtuse. Corner of mouth vertical below anterior edge of posterior nostril. Posterior end of maxilla weakly curved downward, not reaching a vertical at front edge of eye, concealed by preorbital when mouth closed. Posterior nostril a narrow slit, at level of dorsal part of eye, anterior nostril an ovate opening, at level of ventral edge of posterior nostril. Posterior nostril about halfway between anterior edge of orbit and ventral edge of preorbital bone. Lips without teeth; upper lip very thick anteriorly, its lower part with several rows of small papillae (absent in small juveniles); lower lip thin, projecting forward and curved ventrally, with one or two rows of papillae forming a fringe; a large symphysial knob. Body scales cycloid with crenulate membranous edge, 36–40 scales in longitudinal series. Scales in transverse rows 12–14, predorsal scales to origin of first dorsal fin 11–12, predorsal scales to origin of second dorsal fin 22–26, circumpeduncular scales

19–20 (Table 2). Scales on head cycloid and arranged irregularly. Interorbital scales large, decreasing in size anteriorly. Dorsal scales on head extending forward nearly to posterior nostrils. Minute scales present on base of all fins, more prominent on the second dorsal, anal, caudal and pectoral fins, covering more than half of second dorsal fin and anal fin. Two consecutive axillary scales lateral on each side of first dorsal fin, posterior axillary scales reaching behind base of last ray of first dorsal fin. Axillary scales also present lateral to origin of pelvic fin reaching about halfway along pelvic-fin spine. An elongate axillary scale present above pectoral fin.

Fish coloration shown in Figure 4. Silvery olive-gray dorsally, silvery white ventrally; scale rows form indistinct stripes; caudal fin bluish gray; pectoral fins yellowish except for anterodorsally, with a purplish black spot at upper base.

Distribution and habitat. Recorded from the Red Sea, where known south from the Gulf of Aqaba, Socotra Island [51], Oman [52], Iran (Bushehr) and western India, south to Seychelles, Mascarene Islands and Tanzania, east to Vietnam and New Caledonia. Usually seen in small schools in shallow water, including coral reefs; juveniles have been found in tidepools.

Remarks. According to phylogenetic analyses performed by Durand and Borsa [3] and herein, *Moolgarda crenilabis* is closely related to a cryptic clade, herein *Moolgarda* cf. *crenilabis* (Figures 1 and 2), both broadly overlapping in distribution and with similar morphological characters. Comments on cryptic clade provided in Discussion.

Toyama et al. [53] examined small-sized specimens of *M. crenilabis* (as *Crenimugil*) and *M. seheli* and provided data from the examination, in which they found that the former species has a thicker upper lip than specimens of *M. seheli*. Senou [54], and Yoshigou [55] also included *M. crenilabis* for Japanese waters. Records from Japan are retained under question because no tissue samples are available from there. The record from Korea *M. crenilabis* (as *Crenimugil*) by Kwun and Myoung [56] is based on misidentification of *Moolgarda* cf. *crenilabis*; their sample, taken from a single specimen, is nested in this clade.

Material examined: Red Sea, Saudi Arabia: SMF 35920 [KAU11-401], 261.0 mm SL, Farasan Island; SMF 35158, (1) 116.8 mm SL, (2) 99.8 mm SL, (3) 98.0 mm SL, (4) 99.8 mm SL, Al Wajh; **Sudan:** Sudan-100, 261.6 mm SL, Dungonab Bay; Sudan-103, 221.0 mm SL, Dungonab Bay; Sudan-105, 311.0 mm SL, Dungonab Bay; Sudan-106, 305.0 mm SL, Dungonab Bay; Sudan-109, 258.4 mm SL, Dungonab Bay. **Eritrea:** Holotype *Mugil fasciatus* MNHN-A-3637, 205.0 mm SL, Massawa.

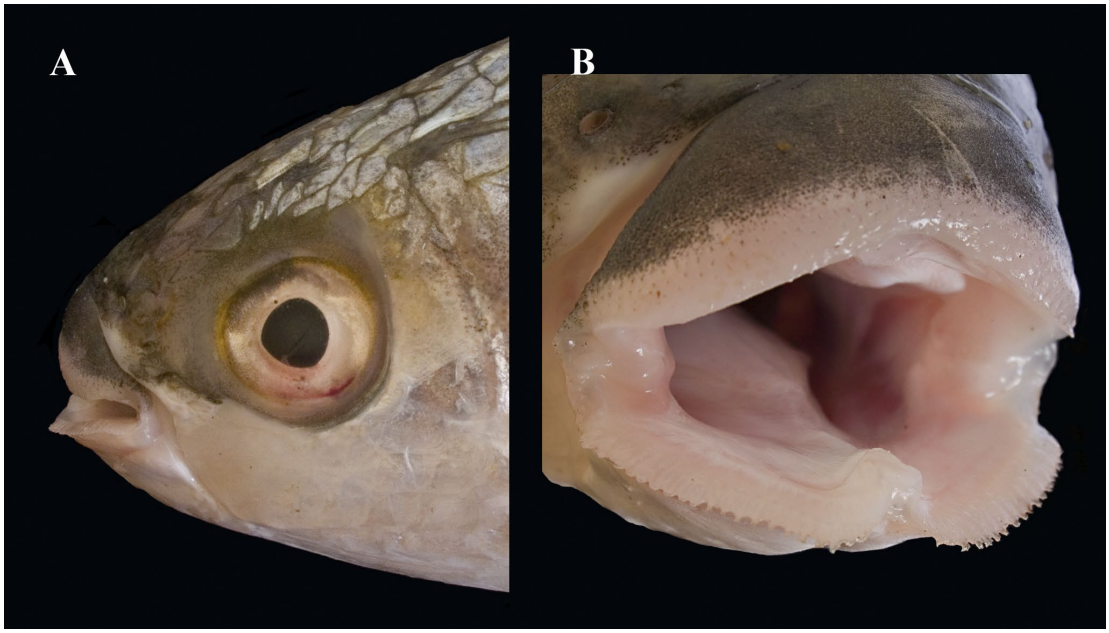

Figure 3. *Moolgarda crenilabis*, not preserved, 280.5 mm SL, Red Sea, Hurghada, (**A**): head close up, lateral view; (**B**): morphology of lips. Photos by S.V. Bogorodsky.

Figure 4. *Moolgarda crenilabis*, SMF uncat (KAU11-401), 261.0 mm SL, Red Sea, Saudi Arabia, Farasan Island, (**A**): a whole specimen; (**B**): head close-up. Photos by S.V. Bogorodsky.

Table 2. Morphometric measurements as percentages of standard length and meristics of examined *Moolgarda crenilabis* including the holotype of *Mugil fasciatus*.

Measurements	KAU11-401	SMF35158 (1)	SMF35158 (2)	SMF35158 (3)	SMF35158 (4)	Sudan-100	Sudan-103	Sudan-105	Sudan-106	Sudan-109	MEAN	MNHN-A-3637
SL (in mm)	261.0	116.8	99.8	98.0	99.8	261.6	221.0	311.0	305.0	258.4		205.0
Total length	123.8	127.5	124.6	130.0	132.2	135.7	127.3	123.8	125.2	130.1	128.0 ± 3.8	130.4
Predorsal length D1	52.2	49.9	49.3	50.6	53.5	53.7	49.9	48.7	47.2	50.2	50.5 ± 2.0	54.0
Predorsal length D2	79.4	77.6	78.4	76.2	79.2	77.7	74.8	71.7	71.2	75.1	76.1 ± 2.8	78.8
Preanal-fin length	77.6	72.7	73.7	73.3	76.4	77.7	75.6	71.7	70.3	72.1	74.1 ± 2.5	75.1
Prepelvic length	40.2	41.3	40.2	40.2	42.9	41.2	40.3	38.4	37.0	36.8	39.8 ± 1.8	40.6
Body width origin PF	19.2	19.3	19.0	19.8	19.6	-	-	-	-	-	19.4 ± 0.3	18.3
Body width origin D1	19.5	18.4	17.0	16.8	17.6	-	-	-	-	-	17.8 ± 1.0	15.4
Body depth origin D1	27.2	29.3	29.5	28.6	28.2	25.1	24.8	22.4	25.4	23.9	26.4 ± 2.3	25.6
Pectoral-fin length	21.0	22.8	22.7	24.2	22.8	21.2	21.9	18.3	19.4	20.8	21.5 ± 1.7	22.1
Pelvic-fin length	14.4	16.6	16.0	17.1	16.0	14.5	13.6	15.1	13.2	13.7	15.0 ± 1.3	14.7
Heigth D2	15.1	15.4	14.5	14.3	14.9	13.3	14.9	13.2	12.0	13.8	14.1 ± 1.0	14.1
Heigth D1	13.6	14.0	13.5	14.3	15.0	13.6	14.3	13.3	12.0	13.0	13.7 ± 0.8	13.5
Heigth anal fin	13.7	16.1	15.9	15.0	15.5	14.0	14.2	14.0	13.3	14.5	14.6 ± 0.9	16.2
Base D2	9.9	9.5	9.8	10.6	11.4	8.9	6.7	7.9	6.6	8.4	9.0 ± 1.5	9.4
Base anal fin	11.0	11.9	10.7	12.0	12.4	8.3	8.3	9.7	9.5	9.1	10.3 ± 1.5	11.2
Pectoral axillary scale length	9.1	7.7	6.9	8.0	7.3	-	-	-	-	-	7.8 ± 0.7	8.3
Caudal peduncle length	16.2	16.8	13.4	13.7	13.8	15.6	18.2	18.9	15.4	17.7	16.0 ± 1.8	13.5
Caudal peduncle depth	12.2	13.9	12.6	13.4	13.0	11.1	11.7	10.3	10.3	10.3	11.9 ± 1.3	11.4
Head length	24.9	28.0	28.6	29.1	29.8	23.5	23.6	23.1	23.1	23.2	25.7 ± 2.7	24.5
Snout length	3.3	5.0	4.3	4.1	4.5	4.9	5.5	6.7	6.5	6.2	5.1 ± 1.1	5.1
Postorbital length	13.8	15.1	15.2	14.1	13.3	14.0	13.5	13.2	13.6	13.1	13.9 ± 0.7	13.6
Orbit diameter	5.9	7.2	8.3	7.5	7.6	6.4	6.7	5.6	5.8	5.3	6.6 ± 0.9	5.3
Interorbital width	13.2	12.8	13.2	11.7	12.7	11.1	10.9	13.0	11.2	10.9	12.1 ± 0.9	11.7
Upper-jaw length	6.5	6.0	5.6	6.4	6.3	5.2	5.4	5.1	6.2	4.4	5.7 ± 0.6	6.0
Thickness of upper lip	2.7	3.2	3.2	2.8	3.0	-	-	-	-	-	3.0 ± 0.2	2.5
Width of mouth	9.4	11.7	9.8	12.0	10.6	8.0	8.7	7.8	8.4	7.3	9.4 ± 1.6	10.0
Head depth	15.6	18.0	17.9	18.7	17.7	14.3	13.2	13.4	15.2	13.5	15.8 ± 2.0	14.6
Head width	15.8	16.6	16.7	16.5	16.8	18.0	16.6	16.3	15.8	16.7	16.6 ± 0.6	15.7
Meristics											Range	
Longitudinal scale rows	38	37	38	37	37	38	36	39	38	-	36–39	37
TV	14	13	13	14	12	13	12	14	14	-	12–14	13
CP	20	19	17	19	20	-	-	-	-	-	17–20	20
PD1	12	11	12	12	12	-	-	-	-	-	11–12	13
PD2	24	24	25	25	26	-	-	-	-	-	24–26	25
Dorsal-fin rays	IV, 10	IV, 10	IV, 10	IV, 10	IV, 10	-	-	-	-	-	IV, 10	IV, 10
Anal-fin rays	III, 10	III, 10	III, 10	III, 10	III, 10	-	-	-	-	-	III, 10	III, 10
Pectoral-fin rays	17	17	17	17	16	-	-	-	-	-	16–17	17

Moolgarda seheli (Fabricius, 1775).

Bluespot Mullet.

Figures 5 and 6, Table 3.

Mugil crenilabis var. seheli Fabricius in (ex Forsskål), 1775 [31], 73 (Al-Luhayya, Yemen, Red Sea; neotype: BMNH 1969.2.8.2).

Mugil seheli—Klunzinger 1870 [34], 827 (Al Quseir, description); Klunzinger 1884 [35], 132 (Red Sea, description); Tortonese 1937 [57], 172 (Massawa, Eritrea, listed).

Liza seheli—Marshall 1952, 242 (Dahab, listed).

Moolgarda seheli—Golani & Lerner 2007 [47], 257 (listed); Fricke 2008 [48], 21 (nomenclature); Golani & Fricke 2018 [8], 119 (listed).

Valamugil seheli—Ben-Tuvia 1975 [41], 16 & 18 (Nabq, Egypt and Eritrea, key); Dor 1984 [42], 193 (listed); Thomson & Luther 1984 [43] (map, description); Goren & Dor 1994 [44], 52 (listed); Thomson 1997 [9], 505 (description, including neotype designation); Golani & Bogorodsky 2010 [49], 39 (listed).

Crenimugil sp. A—Durand & Borsa 2015 [3], 268 (phylogenetic tree).

Diagnosis. Second dorsal-fin rays 9–10 (usually 10); anal-fin rays 9–10; scales cycloid with crenulate membranous edge, 36–40 in longitudinal series; upper lip not thick, with series of minute teeth; ventral edge of preorbital weakly concave at corner of mouth, posterior end of maxilla concealed when mouth closed; origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin; second dorsal fin subequal in height to first dorsal fin but slightly shorter than anal fin; reaches 410 mm SL.

Description. Body moderately elongate, robust, body depth at origin of first dorsal fin 3.5–4.3 in SL and caudal peduncle compressed. Head width slightly greater than head depth, head length 3.4–4.1 in SL. Snout relatively blunt, shorter than orbit diameter, eye diameter 3.8–4.7 in head length. Interorbital region wide and almost flat, its width about 1.6–2.3 in eye diameter and subequal to postorbital length. First dorsal fin with IV spines, second fin with 9–10 (usually 10) rays. Origin of first dorsal fin usually midway or closer to base of caudal fin than to tip of snout. Origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin. Second dorsal fin subequal in height to anal fin but slightly higher than first dorsal fin. Anal fin with III spines and 9–10 rays. Outer margin of second dorsal and anal fins emarginate. Pectoral-fin rays 16–18. Tip of pectoral fin not reaching or just reaching a vertical at origin of first dorsal fin and not behind tip of pelvic-fin spine. If laid forward, pectoral fin not reaching anterior edge of eye. Tip of pelvic fin at vertical of origin of first dorsal fin. Caudal fin forked. Pyloric caeca 7–9 [30].

Adipose eyelid a narrow rim around eye, adipose tissue covers larger area anterior to eye reaching posterior nostril. Preorbital fills space between eye and mouth. Preorbital serrated along antero-ventral to posterior edge starting from above corner of mouth. Ventral edge of preorbital weakly concave, not kinked, at corner of mouth. Posterior end of preorbital obtuse. Corner of mouth a vertical below anterior edge of posterior nostril. Posterior end of maxilla weakly curved downward, not reaching a vertical at front edge of eye, concealed by preorbital when mouth closed. Posterior nostril a narrow slit, at level of dorsal part of eye, anterior nostril an ovate opening, at level of ventral edge of posterior nostril. Posterior nostril about halfway between anterior edge of orbit and ventral edge of preorbital bone. Upper lip not thick, margin of lips thin, with a series of minute teeth; symphysial knob large.

Body scales cycloid with crenulate membranous edge, 36–40 scales in longitudinal series. Scales in transverse rows 12–14, predorsal scales to origin of first dorsal fin 11–13, predorsal scales to origin of second dorsal fin 24–25, circumpeduncular scales 19–20 (Table 3). Scales on head cycloid and arranged irregularly. Interorbital scales large, decreasing in size posteriorly. Dorsal scales on head extending forward nearly to posterior nostrils. Minute scales present on base of all fins, more prominent on the second dorsal, anal, caudal and pectoral fins, covering more than half of second dorsal fin and anal fin. Two consecutive axillary scales lateral on each side of first dorsal fin, posterior axillary scales reaching behind base of last ray of first dorsal fin. Axillary scales also present lateral

to origin of pelvic fin reaching about halfway along pelvic-fin spine. An elongate axillary scale present above pectoral fin.

Fish coloration shown in Figure 5. Silvery gray dorsally, shading to silvery on sides and ventrally, with narrow dark stripes on scale rows; median fins bluish gray; pectoral fins pale yellowish, with a deep blue to black spot at upper base.

Distribution and habitat. Recorded in the Red Sea, where known south of the Gulf of Aqaba and Gulf of Suez, and Socotra Island to the Arabian/Persian Gulf and Pakistan, south to Seychelles and South Africa, east to Mariana Islands and Fiji; also reported in Japan (summarised in Toyama et al. [53]). Usually seen in small schools in shallow water, including coral reefs and estuaries; juveniles have been found in tidepools or brackish habitats.

Remarks. *Moolgarda seheli* is characterised by having a relatively thin upper lip bearing minute teeth at the margin. The species was placed in different genera, *Crenimugil*, *Moolgarda* and *Valamugil*. Because previous and present studies confirmed the placement of *M. crenilabis* and *M. seheli* in one genus a thick upper lip bearing rows of papillae cannot be regarded as a generic identification.

Material examined: Red Sea, Saudi Arabia: KAUMM 476 [KAU13-121], 257.0 mm SL, Al Wajh; SMF 35921 [KAU13-122], 308.3 mm SL, Al Wajh; SMF 35919 [KAU13-461], 105.4 mm SL, Al Wajh; KAUMM 475 [KAU13-463], 107.9 mm SL, Al Wajh; SMF 35922 [KAU17-159], 250.0 mm SL, Farasan Island; SMF 39688, 112.1 mm SL, Al Wajh. **Australia**: AMS IB.1568, 91.5 mm SL, Western Australia, Monte Bello Is (Figure 6).

Table 3. Morphometric measurements as percentages of standard length and meristics of examined *Moolgarda seheli* including *Moolgarda pura* (based on Whitley [10]). Asterisks indicate that in the original description of *Moolgarda pura* Whitley [10] reported 9 fin rays each in the second dorsal and anal fin respectively. However, his depiction ([10]: Figure 8) indicates the presence of 10 fin rays in both fins.

Measurements	KAU13-121	KAU13-122	KAU13-461	KAU13-463	KAU17-159	SMF39688	MEAN	AMS-IB.1568	*Moolgarda pura*
SL (in mm)	257.0	308.3	105.4	107.9	250.0	112.1		92.8	390
Total length	130.0	129.4	131.5	133.6	132.8	131.2	131.4 ± 1.5	125.9	125.6
Predorsal length D1	55.7	52.9	52.5	52.1	51.9	48.9	52.3 ± 2.0	53.8	-
Predorsal length D2	75.9	77.8	76.2	76.5	79.7	76.2	77.0 ± 1.3	77.0	-
Preanal-fin length	73.5	74.0	75.6	77.5	76.4	72.4	74.9 ± 1.8	75.0	-
Prepelvic length	41.1	39.1	40.0	42.4	40.5	42.0	40.8 ± 1.1	44.8	-
Body width origin PF	18.3	18.3	17.7	18.9	18.4	19.4	18.5 ± 0.5	19.2	-
Body width origin D1	18.6	17.6	13.8	14.1	15.7	17.4	16.2 ± 1.8	14.1	-
Body depth origin D1	27.4	23.5	25.6	28.1	28.0	28.6	26.9 ± 1.8	27.4	23.6
Pectoral-fin length	23.9	22.9	23.9	24.3	22.9	24.4	23.7 ± 0.6	23.4	22.1
Pelvic-fin length	15.7	15.3	17.5	17.6	15.3	16.7	16.3 ± 1.0	16.7	-
Heigth D2	15.1	14.0	16.5	15.5	13.6	14.4	14.9 ± 1.0	14.8	-
Heigth D1	13.8	12.2	15.8	14.4	13.4	16.1	14.3 ± 1.3	15.3	-
Heigth anal fin	15.2	13.9	17.0	15.9	14.3	15.6	15.3 ± 1.0	16.9	-
Base D2	10.6	11.2	9.7	10.6	10.9	12.5	10.9 ± 0.8	10.8	-
Base anal fin	12.2	11.0	11.0	13.0	13.4	12.4	12.2 ± 0.9	11.9	-
Pectoral axillary scale length	7.9	9.6	7.0	7.0	8.8	6.9	7.9 ± 1.0	8.0	-
Caudal peduncle length	18.4	16.7	-	15.5	17.2	16.6	16.9 ± 0.9	16.4	-
Caudal peduncle depth	12.3	11.6	12.5	12.5	12.9	13.9	12.6 ± 0.7	12.0	10.0
Head length	25.0	24.3	28.4	28.2	27.2	29.0	27.0 ± 1.8	29.4	25.6
Snout length	4.0	4.1	4.6	4.5	4.1	5.5	4.4 ± 0.5	5.2	6.2
Postorbital length	13.4	14.4	15.6	15.9	14.4	15.2	14.8 ± 0.9	15.7	14.1
Orbit diameter	5.6	5.4	7.5	7.0	5.7	7.6	6.5 ± 0.9	8.6	4.4
Interorbital width	12.3	12.6	12.2	13.0	12.8	12.7	12.6 ± 0.3	12.6	12.3
Upper-jaw length	6.7	6.8	7.1	6.8	7.2	6.9	6.9 ± 0.2	7.0	-
Thickness upper lip	1.7	1.3	-	-	1.4	1.6	1.5 ± 0.2	2.3	-
Width of mouth	10.4	10.2	11.4	11.5	11.1	12.5	11.2 ± 0.8	9.9	-
Head depth	14.6	14.9	17.9	17.0	14.8	16.6	15.9 ± 1.3	17.1	-
Head width	14.9	14.5	18.0	18.1	15.2	17.8	16.4 ± 1.6	-	17.7
Meristics							Range		
Longitudinal scale rows	40	40	38	39	37	38	37–40	39	36
TV	14	12	13	14	-	12	12–14	12	14
CP	20	20	20	19	20	20	19–20	20	-
PD1	13	12	11	13	12	12	11–13	12	14
PD2	25	24	25	25	24	24	24–25	25	26
Dorsal-fin rays	IV, 10	IV, 10	IV, 10	IV, 10	IV, 10	IV, 10	IV, 10	IV, 10	IV, 9 *
Anal-fin rays	III, 10	III, 10	III, 10	III, 10	III, 10	III, 10	III, 10	III, 10	III, 9 *
Pectoral-fin rays	18	17	17	17	16	16	16–18	17	17

Figure 5. *Moolgarda seheli*, SMF uncat (KAU17-159), 250.0 mm SL, Red Sea, Saudi Arabia, Farasan Island, (**A**): a whole specimen; (**B**): head close-up. Photos by S.V. Bogorodsky.

Figure 6. *Moolgarda seheli* from the type locality of *M. pura*, AMS IB.1568, 91.5 mm SL, Western Australia. Photo by A. Hay.

***Moolgarda tade* (Fabricius, 1775).**

Longfin Mullet.

Figure 7, Table 4.

Mugil crenilabis tade Fabricius in Niebuhr (ex Forsskål), 1775 [31], 74 (Red Sea; no type known).

Mugil tade—Rüppell 1852 [58], 11 (description); Klunzinger 1870 [34], 828 (Al Quseir, description); Klunzinger 1884 [35], 133, Figure 3 (Red Sea, description); Tortonese 1935 [57], 171 (Massawa, Eritrea, listed); Roux-Estève & Fourmanoir 1955 [37], 196 (Abu Latt, Saudi Arabia, listed).

Liza tade—Dor 1984 [42], 191 (listed); Goren & Dor 1994 [44], 51 (listed); Thomson & Luther 1984 [43] (map, description).

'Chelon' tade—Fricke 2008 [48], 20 (nomenclature).

Planiliza tade—Golani & Fricke 2018 [8], 119 (listed).

Crenimugil buchanani (non Bleeker)—Durand & Borsa 2015 [3], 269 (phylogenetic tree).

Diagnosis. Second dorsal-fin rays 10; anal-fin rays 10; scales cycloid with crenulate membranous edge, 33–37 in longitudinal series; upper lip moderately thick, lips without teeth; ventral edge of preorbital weakly concave at corner of mouth, posterior end of maxilla concealed when mouth closed; origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin; second dorsal fin 1.4–1.8 times higher than first dorsal fin and subequal in height to anal fin; reaches 480 mm SL.

Description. Body moderately elongate, robust, body depth at origin of first dorsal fin 3.6–4.0 in SL and caudal peduncle compressed. Head depth subequal to head width, head length 4.1–4.5 in SL. Snout relatively blunt, equal to or slightly longer than orbit diameter, eye diameter 4.1–4.8 in head length. Interorbital region wide and almost flat, its width about 2 times eye diameter, and subequal to postorbital length. First dorsal fin with IV spines, second fin with 10 rays. Origin of first dorsal fin usually midway between base of caudal fin and tip of snout. Origin of second dorsal fin above or slightly posterior to vertical at origin of anal fin. Second dorsal and anal fins high, falcate. Second dorsal fin 1.4–1.8 times higher first dorsal fin and subequal in height to anal fin. Anal fin with III spines and 10 rays. Outer margin of second dorsal and anal fins deeply emarginate. Pectoral-fin rays 17–19. Tip of pectoral fin not reaching or just reaching a vertical at origin

of first dorsal fin and not behind tip of pelvic-fin spine. If laid forward, pectoral fin not reaching anterior edge of eye. Tip of pelvic fin at vertical of origin of first dorsal fin. Caudal fin deeply emarginate.

Adipose eyelid a narrow rim around eye, adipose tissue covers larger area anterior to eye reaching posterior nostril. Preorbital fills space between eye and mouth. Preorbital serrated along antero-ventral to posterior edge starting from above corner of mouth (Figure 7). Ventral edge of preorbital weakly concave, not kinked, at corner of mouth. Posterior end of preorbital obtuse. Corner of mouth a vertical below anterior edge of posterior nostril. Posterior end of maxilla weakly curved downward, not reaching a vertical at front edge of eye, concealed by preorbital when mouth closed. Posterior nostril a narrow slit, at level of dorsal part of eye, anterior nostril an ovate opening, at level of ventral edge of posterior nostril. Posterior nostril about halfway between anterior edge of orbit and ventral edge of preorbital bone. Upper lip moderately thick, margin of lips without teeth; symphysial knob large.

Body scales cycloid with crenulate membranous edge, 32–36 scales in longitudinal series. Scales in transverse rows 11–13, circumpeduncular scales 19–20 (Table 4). Scales on head cycloid and arranged irregularly. Interorbital scales large, decreasing in size posteriorly. Dorsal scales on head extending forward to posterior nostrils. Minute scales present on base of all fins, more prominent on the second dorsal, anal, caudal and pectoral fins, covering more than half of second dorsal fin and anal fin. Two consecutive axillary scales lateral on each side of first dorsal fin, posterior axillary scales reaching behind base of last ray of first dorsal fin. Axillary scales also present lateral to origin of pelvic fin reaching about halfway along pelvic-fin spine. An elongate axillary scale present above pectoral fin.

Fish coloration shown in Figure 7. Silvery gray on back, silvery on sides and ventrally, scale rows form longitudinal stripes; pectoral fins yellowish, except semitranslucent posterior margin, with a black spot at upper base.

Distribution and habitat. Recorded in the Red Sea, where known south to southern Egypt, to Gulf of Oman (Iran), south to Madagascar and South Africa, east to the Philippines and New Caledonia. Yoshigou [55] described specimens with falcate second dorsal and anal fins from Japan under the name *Moolgarda malabarica* (Shaw, 1804). Samples of tissue are needed to assess whether Japanese specimens are *M. tade* or represent a distinct species. Usually seen in small schools in coastal waters and estuaries, juveniles have been found in tidepools, depth range 1–20 m.

Remarks. The name tade has been a matter of confusion for a long time. In his draft, Forsskål used the Arabic name 'tâde' as a substitute for a Latin name possibly to be selected at a later date, before the description was later compiled by Fabricius. Fabricius in Niebuhr [31] described the new species in two different versions, as a variety *Mugil crenilabis tâde* in the index on p. XIV, and as *Mugil crenilabis*, variety *tâde or ædda* on p. 74. It is assumed that it is meant to be a variety of *Mugil crenilabis* in both versions and the name would be available from the index as *Mugil crenilabis tade*. Fricke [48] stated the name is accompanied by a diagnosis and would be available by indication (ICZN, Art. 12.2.2) as *Mugil crenilabis tade* Fabricius [ex Forsskål] in Niebuhr, 1775, with the actual name *Chelon tade* (Fabricius [ex Forsskål] in Niebuhr, 1775). Although the diagnosis is very brief, it bears one important character for the species diagnose: presence of high second dorsal fin (Fabricius 1775 [31], p. 74: 'Spina dors. secunda longior prima'). Klunzinger ([35], pl. X, Figure 3) provided an additional description of the species and figured a specimen from Al-Quseir with high second dorsal and anal fins. Ben-Tuvia [41] noted that two specimens of *Liza subviridis* from Eritrea match the description of *Mugil tade* given by Klunzinger [35]. Thomson [9] described the species in the genus *Liza*, but his description clearly matches species of the genus *Osteomugil* (i.e., adipose tissue covering most of iris and origin of second dorsal fin approximately below one-half of anal-fin base). He compared *L. tade* with *L. subviridis* and *L. parsia* (Hamilton, 1822) and placed *Mugil planiceps* Valenciennes, 1836 in the synonymy. Harrison and Senou [28] included *Liza planiceps* in their chapter and placed *M. tade* in the list of synonyms. Kottelat [11] attributed the authorship of *L. tade* to Bloch

& Schneider 1801 and listed *Moolgrada malabarica* as valid name and *Mugil buchanani*, *M. ceylonenis* Günther, 1861 and *M. pedaraki* Valenciennes, 1836 as synonymy names. Durand and Borsa [3], based on the result of their genetic analyses and the retrieved position of specimens NRM-58400 and NRM-58557 from Myanmar, morphologically identified as *Liza planiceps*, a species name considered as a junior synonym of *Liza tade* by Thomson [9], moved *Mugil tade* into the genus *Planiliza* (named as *P.* sp. I). They additionally included specimens with high second dorsal and anal fins in their analysis as *Crenimugil buchanani*. Golani and Fricke [8] in their checklist of the Red Sea fishes retained *M. tade* in *Planiliza*.

Close examination of specimens from Sudan with long, falcate, second dorsal and anal fins and their inclusion in the comparative genetic analysis demonstrated that the species is nested within *Moolgarda* alongside with *M. crenilabis* and *M. seheli*. Specimens from India are nested with other specimens of *M. tade* in the same clade. Because no other species with long falcate second dorsal and anal fins were found in the region and all Indian specimens with this morphology share the same BIN BOLD:AAE3561 [59], as Red Sea specimens (Figure 1), we propose to place the following species described from India and Sri Lanka (*M. buchanani*, *M. ceylonensis*, *M. malabarica* and *M. pedaraki*) in the synonymy with *M. tade*.

Material examined: Sudan: (VMH1/Sudan-900), 376.0 mm SL, Suakin Archipelago; (VMH2/Sudan-901), 375.0 mm SL, Suakin Archipelago; (VMH3/Sudan-902), 345.0 mm SL, Suakin Archipelago; (VMH4/Sudan-903), 394.0 mm SL, Suakin Archipelago; (VMH5/Sudan-904), 361.0 mm SL, Suakin Archipelago.

Figure 7. *Moolgarda tade*, VMH 1 (Sudan-900), 400.5 mm SL, Red Sea, Sudan, Suakin Archipelago. Photo by Shaker S. Shaheen.

Table 4. Morphometric measurements as percentages of standard length and meristics of examined *Moolgarda tade*.

Measurements	Sudan-900	Sudan-901	Sudan-902	Sudan-903	Sudan-904	Mean
SL (in mm)	376.0	375.0	345.0	394.0	361.0	
Total length	138.8	133.1	136.8	132.7	129.4	134.2 ± 3.3
Predorsal length D1	51.5	48.1	48.0	49.0	49.4	49.2 ± 1.3
Predorsal length D2	76.6	73.4	72.6	72.7	72.0	73.5 ± 1.6
Preanal-fin length	76.4	73.7	71.0	72.5	66.7	72.1 ± 3.2
Prepelvic length	38.6	37.1	37.1	36.7	35.7	37.0 ± 0.9
Body width origin PF	-	-	-	-	-	-
Body width origin D1	-	-	-	-	-	-
Body depth origin D1	26.4	26.2	27.7	25.7	25.1	26.2 ± 0.9
Pectoral-fin length	23.5	22.6	24.3	22.7	23.0	23.2 ± 0.6
Pelvic-fin length	17.2	16.1	19.0	15.4	15.9	16.7 ± 1.3
Heigth D2	21.2	21.2	23.4	20.4	19.7	21.2 ± 1.3
Heigth D1	13.8	14.1	13.2	12.7	13.8	13.5 ± 0.5
Heigth anal fin	19.9	18.8	21.8	18.0	19.7	19.7 ± 1.3
Base D2	8.6	9.3	8.9	8.7	9.3	9.0 ± 0.3
Base anal fin	11.0	9.6	9.5	9.1	10.9	10.0 ± 0.8
Pectoral axillary scale length	-	-	-	-	-	-
Caudal peduncle length	19.5	19.5	17.9	16.5	17.5	18.2 ± 1.2
Caudal peduncle depth	12.3	11.9	12.4	12.6	12.3	12.3 ± 0.2
Head length	23.5	22.2	24.3	22.6	23.0	23.1 ± 0.7
Snout length	6.3	5.9	5.7	5.5	6.2	5.9 ± 0.3
Postorbital length	15.1	13.4	13.8	14.4	13.8	14.1 ± 0.6
Orbit diameter	4.9	5.5	6.0	5.3	5.4	5.4 ± 0.3
Interorbital width	11.3	10.8	11.1	10.4	10.7	10.9 ± 0.3
Upper-jaw length	5.5	5.2	5.1	5.2	5.2	5.2 ± 0.2
Thickness upper lip	-	-	-	-	-	-
Width of mouth	9.5	9.0	9.0	9.7	8.4	9.1 ± 0.5
Head depth	12.4	11.6	12.2	12.7	11.9	12.1 ± 0.4
Head width	13.6	14.9	16.0	16.2	15.9	15.3 ± 1.0
Meristics						Range
Longitudinal scale rows	33	34	33	32	36	32–36
TV	11	12	12	13	13	11–13
CP	20	-	-	-	-	-
PD1	-	-	-	-	-	-
PD2	-	-	-	-	-	-
Dorsal-fin rays	-	-	-	-	-	-
Anal-fin rays	-	-	-	-	-	-
Pectoral-fin rays	-	-	-	-	-	-

4. Key to the Red Sea species of *Moolgarda*

1a. Second dorsal fin 1.4–1.8 times higher than first dorsal fin, second dorsal and anal fins falcate, subequal in height; scales in longitudinal series 33–37. . . . . ***M. tade***
1b. Second dorsal fin subequal in height to first dorsal fin and slightly lower than anal fin; scales in longitudinal series 36–40. . . . . **2**
2a. Upper lip very thick anteriorly, its lower part with several rows of small papillae; lower lip with fringed anterior edge. . . . . ***M. crenilabis***
2b. Upper lip thin, its lower part not papillated; anterior edge of lower lip not fringed. . . . . ***M. seheli***

5. Discussion

The Mugilidae is a family of shallow-water fishes distributed in tropical and temperate seas circumglobally. They typically inhabit marine or brackish waters, but few species live in freshwater environments. For a long time, the classification of mugilid species has

been chaotic, despite an effortful revision of the whole family by Thomson [9], in which he included descriptions of 14 genera and 62 species. Later studies, based on molecular data, proposed numerous changes to the generic and species taxonomy [1,3,4]. Currently, 72 species are recognized in 26 genera [7]. However, genetic data suggest that many cryptic species are present in all major mugilid clades [3,12]. Several recent studies have already contributed to a better understanding of mugilid phylogeny, systematics and taxonomy, especially by describing some of the cryptic species found in this family [4–6]. This study presents further data, helping to unravel the taxonomic issues of mugilids. The genus name *Moolgarda* is revived for the clade containing nine lineages, three applied to described species *M. crenilabis*, *M. seheli* and *M. tade*, as well as one species with a doubtful affiliation, *M.* cf. *crenilabis*, and five putative species abbreviated in the present study as *M.* sp. C, *M.* sp. D, *M.* sp. E, *M.* sp. F and *M.* sp. H.

In previous genetic analyses, *Crenimugil* sp. A was retrieved as a monophyletic clade within the *Crenimugil seheli* species complex [3,12]. This evolutionary clade was identified as *Moolgarda seheli* in the present study. Originally described from the Red Sea, this species has a wide-ranging distribution from the Red Sea south to South Africa, across the Indian and Western Pacific Ocean as far east as Fiji. The morphological characters provided here are mainly taken from specimens from the Red Sea, and some variation along the distribution area is expected. The genetic analysis also shows a low genetic divergence among different locations (e.g., Red Sea/Northern Indian Ocean and the Western Pacific Ocean) and the status as a single widespread species is supported by all species delimitation approaches used in this study. Further studies should provide additional morphological data from across the entire range of *M. seheli* in combination with a more detailed genetic analysis. According to Thomson [9] and Kottelat [11], the following nominal species were placed in the synonymy with *M. seheli*: *Mugil axillaris* Valenciennes, 1836 (Mauritius and New Guinea), *Mugil bleekeri* Günther, 1861 (Indonesia), *Mugil caeruleomaculatus* Lacepède, 1803 (no locality), *Mugil cylindricus* Valenciennes, 1836 (Java, Indonesia), *Mugil decemradiatus* Günther, 1861 (Jakarta, Indonesia), *Mugil delicatus* Alleyne & Macleay, 1877 (Queensland, Australia), *Liza formosae* Oshima, 1922 (Taiwan), *Mugil melancranus* Richardson, 1846 (China), *Moolgarda pura* Whitley, 1945 (Western Australia), *Mugil splendens* De Vis, 1885 (Queensland, Australia) and *Mugil suppositus* Günther, 1861 (Malaysia).

Durand and Borsa [3] analysed specimens from the Seychelles to French Polynesia which they identified as *Crenimugil crenilabis*. In their genetic analyses, they retrieved a second clade, closely related to *C. crenilabis*, which they named *C.* sp. B. Morphological examination and genetic analyses of specimens from the type locality of *M. crenilabis*, the Red Sea, revealed that in actuality *C.* sp. B represents *M. crenilabis*, while the identity of *Crenimugil crenilabis* (sensu Durand and Borsa 2015 [3]) remains doubtful at this time and here is referred to as *M.* cf. *crenilabis*. While Red Sea specimens and representatives of *M.* cf. *crenilabis* from the Indo-Pacific show a similar morphology regarding their upper and lower lips, specimens of *M. crenilabis* outside the Red Sea curiously show closer morphological similarities to *M. seheli*, which raises questions of the spatial congruence of genetic and morphological data for these species. We suggest that the phylogenetic relationships between these evolutionary clades should be further investigated before a definite species name is assigned to *M.* cf. *crenilabis*. If *M.* cf. *crenilabis* is to be recognized as a valid species in future studies, the nominal species *Mugil cirrhostomus* Forster, 1801 (described from the Central Pacific) may provide a species name for the widely distributed *M.* cf. *crenilabis* (Western Indian Ocean, except Red Sea, east to French Polynesia). In the past, multiple nominal species were synonymized with *M. crenilabis*: *Mugil cirrhostomus*, *Mugil fasciatus* Valenciennes, 1836 (Red Sea), *Mugil macrocheilos* Bleeker, 1854 (Cocos Keeling Islands), *Mugil neocaledonicus* Castelnau, 1873 (New Caledonia) and *Mugil rueppellii* Günther, 1861 (Red Sea) [9,11].

Up to now, the generic assignment of *Mugil tade* was confusing. While Fabricius in Niebuhr [31] classified this species as a variation of *M. crenilabis*, it was later placed in the genera *Liza* (e.g., [42–44]), *Chelon* (e.g., [48]) and *Planiliza* (e.g., [8]). We were able to

identify a monophyletic evolutionary clade within the genus *Moolgarda* which presents all characters previously described by Fabricius in Niebuhr [31] and therefore we assigned the species name *M. tade* to this clade. The following nominal species are recognised as synonyms of *M. tade* according to Kottelat [11] and the present study: *Mugil buchanani* (Calcutta, India), *Mugil ceylonensis* (Sri Lanka), *Mullus malabaricus* (India), *Mugil pedaraki* (Visakhapatnam, India) and *Mugil radians* Castelnau, 1861 (South Africa).

Aside from *Moolgarda crenilabis*, *M. seheli* and *M. tade* (previously recognized as *Crenimugil buchanani*), there was one other species recognized as valid within the genus *Crenimugil*: *C. heterocheilos* (Bleeker, 1855) [7]. Bleeker [60] originally described the species based on specimens from Indonesia and noted its similarity to *Mugil crenilabis* and *Mugil cirrhostomus*. After Schultz [26] created the new genus *Crenimugil* based on the distinctive characteristics of *Moolgarda crenilabis*, i.e., toothless lips, upper lip thick with margin bearing several rows of small papillae and margin of lower lip distinctly fringed, Roberts [61] added the species *Crenimugil heterocheilos* to this genus because of its thick upper lip that bears rows of papillae. The latter differs from *Moolgarda crenilabis* in having rows of hard papillae laterally on the upper lip that are arranged in ridges and the edge of the lower lip not crenulated. Because of the strong resemblance of *M. crenilabis* and *C. heterocheilos*, the latter species is retained as valid in the genus *Moolgarda* herein (as *Crenimugil* in [7,9,28]), yet at this point it remains unclear to which of the five unnamed evolutionary clades within the genus *Moolgarda* it can be assigned. *Moolgarda heterocheilos* is supposedly distributed in the Indo-West Pacific and ranges from Japan to New Caledonia and Indonesia to French Polynesia [7]. Two nominal species *Mugil banksi* Seale, 1910 (from the Philippines) and *Mugil papillosus* Macleay, 1883 (from Papua New Guinea) are currently placed in the synonymy with *Moolgarda heterocheilos* [7,9,11].

Specimens of the genetic clade *M.* sp. C are similar to *M. tade* and characterized by the second dorsal fin being slightly higher than the first dorsal fin and the anal fin slightly longer than the second dorsal fin. While there are some nominal species that also share these characteristics such as *Mugil delicatus*, examination of specimens of this as well as the remaining unnamed clades *M.* sp. E and *M.* sp. F are necessary but a matter of further research. Distribution of each lineage is included in Table 5.

Table 5. Distribution of lineages/species.

Current Species ID	Proposed Name	Name of Lineage in Durand & Borsa (2015) [3]	Distribution Based on DNA (Including Private Sequences) and Verified Records	Remarks
Moolgarda crenilabis (Forsskål, 1775)	-	*Crenimugil* sp. B	Red Sea, Socotra, Oman (Randall 1995 [52]), Iran (Bushehr), India (Kerala), Seychelles, Reunion, Mauritius, Tanzania, Sri Lanka, Indonesia, Vietnam, New Caledonia	
Moolgarda cf. *crenilabis* (Forsskål, 1775)	*Moolgarda cirrhostoma* (Forster, 1801)	*Crenimugil crenilabis*	South Africa, Mozambique, Mauritius, Seychelles, Maldives, Coral Sea, Australia (Queensland), Korea (Kwun & Myoung 2019 [56]), Mariana Islands, New Caledonia, Tahiti, Marquesas Islands	The species was described from central Pacific in Cook's voyage. This is a single species known there; hence, this name can apply to the lineage related to *M. crenilabis*
Moolgarda seheli (Fabricius, 1775)	-	*Crenimugil* sp. A	Red Sea, Gulf of Aden, Socotra, Oman, Arabian/Persian Gulf, Pakistan, South Africa, Seychelles, Reunion, Maldives, Indonesia, Papua New Guinea, Philippines, Vietnam, Taiwan, Mariana Islands, Australia (Queensland), New Caledonia, Fiji	

Table 5. *Cont.*

Current Species ID	Proposed Name	Name of Lineage in Durand & Borsa (2015) [3]	Distribution Based on DNA (Including Private Sequences) and Verified Records	Remarks
Moolgarda tade (Forsskål, 1775)	-	*Crenimugil buchanani*	Red Sea, Iran (Gulf of Oman), Kenya, Madagascar, Seychelles, Mauritius, South Africa, India, Thailand, Indonesia, Philippines, New Caledonia	*Mugil buchanani*, *Mullus malabarica* and *Mugil pedaraki*, described from east coast of India, are junior synonyms.
Moolgarda sp. C	*Moolgarda delicata* (Alleyne & Macleay, 1877)	*Crenimugil* sp. C	Australia (Queensland, Northern Territory), Malaysia, Indonesia (Bali, Kalimantan), Philippines, Vietnam	Similar to *M. tade* in having falcate D2 but the fin is slightly shorter than in *M. tade*
Moolgarda sp. D	*Moolgarda heterocheilos* (Bleeker, 1855)	*Crenimugil* sp. D	Indonesia, Papua New Guinea, Philippines, Taiwan, New Caledonia (Séret 1997 [62]), Fiji	Upper lip with dermal ridges of papillae
Moolgarda sp. E	-	-	Indonesia (Sumatra), Thailand, Malaysia, Vietnam	
Moolgarda sp. F	-	-	New Caledonia	
Moolgarda sp. H	-	-	eastern Indonesia, Papua New Guinea	

The present study clearly demonstrates that research in contribution of the taxonomy and relationships of genera and species of the family Mugilidae is a continuing process and an additional effort is needed to revise some problematic genera of the family, including species names for the still unnamed evolutionary clades in the genus *Moolgarda*.

6. Conclusions

The results of the study demonstrated that some mugilid fishes variously reported in genera *Crenimugil*, *Moolgarda* and *Valamugil* should be assigned to a single genus. The genus *Moolgarda* is revived and its priority over *Crenimugil* and *Valamugil* is shown. Results, based on a comprehensive mitochondrial and nuclear phylogeny and species delimitation, confirmed the presence of nine genetic lineages in the genus. *Moolgarda crenilabis*, *M. seheli* and *M. tade* are redescribed based on specimens from the Red Sea, type locality of these species. Overall, the results of the study will help improve the knowledge of the diversity and distribution of one of the most important groups of brackish-water and coastal species of the family Mugilidae in the Indo-West Pacific.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16060325/s1, Table S1: species names, locations, BOLD and GenBank accession numbers and BIN ID (BOLD) for the mullet sequences included in the phylogenetic tree presented in Figure 1. Table S2: List of the primers and annealing temperatures used in the PCR experiments to amplify the six gene fragments. References [4,13,63–65] are cited in the Supplementary Materials.

Author Contributions: S.V.B., P.T., T.J.A. and J.-D.D. conceived the study. S.V.B., P.T., J.-D.D. and Z.N.M. undertook field surveys, carried out morphological examinations and contributed to laboratory work. J.-D.D. and T.J.A. carried out the laboratory work. J.-D.D. performed the phylogenetic analysis. J.-D.D., S.V.B., P.T., T.J.A. and H.S. co-wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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