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Systematics of the grey mullets (Teleostei: Mugiliformes: Mugilidae): molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy

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Running title: Molecular systematics of the Mugilidae
Abstract

The family Mugilidae comprises mainly coastal marine species that are widely distributed in all tropical, subtropical and temperate seas. Mugilidae species are generally considered to be ecologically important and they are a major food resource for human populations in certain parts of the world. The taxonomy and systematics of the Mugilidae are still much debated and based primarily on morphological characters. In this study we provide the first comprehensive molecular systematic account of the Mugilidae using phylogenetic analyses of nucleotide sequence variation at three mitochondrial loci (16S rRNA, cytochrome oxidase I, and cytochrome b) for 257 individuals from 55 currently recognized species. The study covers all 20 Mugilidae genera currently recognized as being valid. The family comprises 7 major lineages that radiated early on from the ancestor to all current forms. All genera that were represented by two species or more, except Cestraeus, turned out to be paraphyletic or polyphyletic. Thus, the present phylogenetic results generally disagree with the current taxonomy at the genus level and imply that the anatomical characters used for the systematics of the Mugilidae may be poorly informative phylogenetically. The present results should provide sound basis for a taxonomic revision of the Mugilidae genera. A proportion of the species with large distribution ranges (including Moolgarda seheli, Mugil cephalus and M. curema) appear to consist of cryptic species, thus warranting further taxonomic and genetic work at the infra-generic level.

Keywords: cryptic species, 16S rRNA, cytochrome oxidase I, cytochrome b, phylogeny
1. Introduction

The Mugilidae (or grey mullets) is a speciose family of Teleostean fishes, which has representatives in various coastal aquatic habitats of the world’s tropical, subtropical and temperate regions (Thomson, 1966). Despite the ecological and economical importance of grey mullet (Thomson, 1966), the taxonomy and evolutionary relationships among the species so far remains largely unresolved (Harrison et al., 2007). A major reason is that most morphological characters classically used in species identification and/or systematics are remarkably similar within the family (Schultz, 1946; Thomson, 1997). Thus, it has been a challenging task to define species and genera and, during the last 130 years, up to 281 nominal species and 45 nominal genera have been proposed for the Mugilidae (Thomson, 1997; Eschmeyer and Fricke, 2011). The number of Mugilidae species has probably been overestimated since most of the earlier taxonomic work relied on the examination of specimens collected locally, without comparing these specimens to morphologically similar species described elsewhere (Thomson, 1954).

The first thorough taxonomic revision of the Mugilidae was produced by Schultz (1946), who mainly used mouth anatomy to define both genera and species. Schultz (1946) validated only ten previously defined Mugilidae genera and described three new ones, a revision that was subsequently questioned [see review in Ghasemzadeh et al. (2004)]. Mugilidae taxonomy and nomenclature have still not been finalized (Harrison et al., 2007), with between 14 and 20 genera being recognized as valid according to the most recent revisions (Thomson, 1997; Ghasemzadeh, 1998; Nelson, 2006). The Integrated Taxonomic Information System recognizes 16 valid genera (http://www.itis.gov/; information retrieved on 16 August 2011), while Eschmeyer and Fricke (2011) list 20 valid genera. Two genera, *Liza* and *Mugil*, currently represent 40% of the species richness within the family Mugilidae (Eschmeyer and Fricke, 2011). The other genera consist of fewer species and 40% (8/20) are monotypic (Eschmeyer and Fricke, 2011). The high proportion of monotypic genera may reflect the general difficulty in classifying Mugilidae species on the basis of the few diagnostic or synapomorphic characters that have been considered so far. Alternatively, this may indicate an ancestral radiation event followed by a long period of stasis.

Anatomical differences among Mugilidae species are not easily interpretable from a cladistic perspective, as shown by the conflicting morpho-anatomical phylogenetic hypotheses proposed by different authors (Fig. 1 A-E). For example, *Rhinomugil*, which was considered by Schultz (1946) as an aberrant genus and was tentatively placed by him at an intermediate position in the Mugilidae tree (Fig. 1 A), was later assessed to be closely related to the genus *Liza* and other reportedly recently derived Mugilidae genera (Thomson, 1997; Ghasemzadeh, 1998). Similarly, Harrison and Howes (1991) and some other authors (Fig. 1 C-E) have suggested that the rudimentary pharyngobranchial organ in *Cestraeus* is a plesiomorphic character. In contrast, Schultz (1946) regarded *Cestraeus* to be a recently derived genus, pointing its highly specialized lips and teeth as supporting evidence (assumed by him to be an apomorphic anatomical feature in the Mugilidae). Thomson (1997) used both internal (intestine, stomach, pyloric caeca) and external (nostrils, teeth, scales, lips, preorbital bones, jaw) anatomical structures to resolve the polytomies remaining in the phylogeny proposed by Harrison and Howes (1991) (Fig 1C). Thomson (1997) suggested that the genera *Chelon*, *Liza* and *Oedalechilus* are closely related (Fig. 1D). These three genera had been synonymized by Shultz (1946), but Harrison and Howes (1991) had assigned them distinct lineages (Fig. 1C) due to divergent views on how to weigh the anatomical characters.

In the last decade, molecular studies have provided many insights into the systematics of fishes at all taxonomic levels (Chen and Mayden, 2010) while phylogeographic studies have provided important insight into evolutionary forces that shape intraspecific genetic diversity (Avise, 2000). The Mugilidae were initially placed in an intermediate position in the Acanthomorph tree because of putatively plesiomorphic
morphological features shared with Atherinomorpha, themselves considered as more basal Teleosteans (Stiassny, 1993), with the Mugilidae actually related to other advanced teleosts within the Percomorpha (Chen et al., 2003, 2007; Mabuchi et al., 2007; Miya et al., 2003). The placement of the Mugilidae in the Acanthomorph tree has been further explored by Smith and Wheeler (2006), Smith and Craig (2007), Setiamarga et al. (2008), and Li et al. (2009).

Phylogenetic relationships within the Mugilidae have largely been based on specimens collected within particular geographic regions, such as India (Menezes, 1992), East Asia (Lee et al., 1995, Liu et al., 2010), America (Fraga et al., 2007), and the Mediterranean (Autem and Bonhomme, 1980; Bel et al., 2008; Caldara et al., 1996; Erguden et al., 2010; Gornung et al., 2007; Imsiridou et al., 2007; Murgia et al., 2002; Papasotiropoulos et al., 2001, 2002, 2007; Rossi et al., 1998a, 2004; Semina et al., 2007; Turan et al., 2005). The above studies have generally demonstrated an early rapid divergence for the Mugil lineage and have led to a questioning of the monophyly of the genera Chelon and Liza (Aurelle et al., 2008). Phylogeographic studies within the Mugilidae have focused on only two species of the genus Mugil, namely M. cephalus (Crosetti et al., 1993, 1994; Heras et al., 2009; Jamandre et al., 2009; Ke et al., 2009; Liu et al., 2009; Livi et al., 2011; Rocha-Olivares et al., 2000; Rossi et al., 1998b; Shen et al., 2011) and M. curema (Fraga et al., 2007; Heras et al., 2006, 2009). In the process, multiple independent lineages have been uncovered within both M. cephalus and M. curema (Aurelle et al., 2008; Fraga et al., 2007; Heras et al., 2009). Based on the above findings, additional efforts are certainly required to resolve the evolutionary relationships within the Mugilidae at both the generic and species levels.

In this study, the phylogenetic relationships within the Mugilidae were investigated based on the analysis of DNA sequence variations from three mitochondrial loci (16S, COI, and cyt b) and using representative taxonomic sampling in order to provide the first comprehensive insight into the systematics of the family. Using the COI gene polymorphism as a marker, Zemlak et al. (2009) have inferred that up to 60% of inshore fish species with an Indo-Pacific distribution might well consist of sibling species. To further address the issue of cryptic species within widely distributed Mugilidae species, emphasis was placed on geographical sampling of a number of species with large geographic distributions, namely Chelon macrolepis, Crenimugil crenilabis, Moolgarda cunnesius, M. sebeli, Mugil cephalus, M. curema and Valamugil buchanani.

2. Materials and Methods

2.1. Data collection and analysis

It was essential to use a broad taxonomic sampling in order to best represent the phylogenetic diversity within the family Mugilidae (Hillis, 1998) and to provide the most accurate insights into relationships between genera. The many uncertainties concerning the validation of some genera or species required sampling of multiple representatives of each genus, and/or species when possible. Nineteen of the 20 Mugilidae genera currently recognized as valid (Eschmeyer and Fricke, 2011) were sampled, using museum specimens where possible. If a specimen could not be identified to species using Thomson’s (1997) descriptions, or FAO species identification sheets (Harrison and Senou, 1999), it was identified to genus only.

The mitochondrial-DNA sequences of a total of 257 Mugilidae individuals (Table 1), together with outgroups comprising an individual of each Abudusdof vaigensis (Perciformes: Pomacentridae), Labracinus cyclophthalmus (Perciformes: Pseudochromidae) and Oryzias latipes (Beloniformes: Adrianichthyidae), were used for phylogenetic analysis. The three outgroup taxa were selected because their complete mito-genomic data were available (GenBank accession nos. AP006016, AP009125 and AP004421, respectively) and
were shown to be closely related to the Mugilidae in recent molecular studies investigating higher-level phylogenetic relationships in the Percomorpha (Chen et al., 2007; Mabuchi et al., 2007).

Some Mugilidae species have a wide geographic distribution and in these instances the species were represented by samples from different oceanic regions. Species falling into this category were *Agonostomus monticola*, *Cebolon macropterus*, *Crenimugil cretilabis*, *Liza alata*, *L. dumerili*, *Moolgarda annenesis*, *M. seheli*, *Mugil cephalus*, *M. curema* and *Valamugil buchanani* (Table 1).

Genomic DNA was extracted from muscle samples or fin clips using standard phenol-chloroform protocols (Sambrook et al., 1989). A portion of each 16S ribosomal RNA gene (16S), cytochrome oxydase I gene (COI), and cytochrome b gene (cyb) was amplified by polymerase-chain reaction (PCR) using the primers listed in Table 2. PCR was carried out in 50 µl reaction volume containing 5 µl 10X reaction buffer (Promega, Charbonnières, France), 1.5 µl MgCl2 (25 mM), 2 µl dNTP (5 mM), 0.5 µl each primer (10 µM), 1 unit GoTaq DNA polymerase (Promega Corporation, Madison, USA) and 1 µl template DNA. PCR conditions were as follows: preliminary denaturation at 92°C for 5 min followed by 35 cycles of strand denaturation at 92°C for 1 min, primer annealing at 50°C for 1 min (16S) or 52°C for 45s (COI and cyb) and primer extension at 72°C for 1.5 min, followed by final extension at 72°C for 5 min. Sequencing was performed by Macrogen Inc. (Seoul, South Korea; http://dna.macrogen.com). All nucleotide sequences were deposited in GenBank (Table 1).

Some *M. curema* individuals were karyotyped using methods described by Nirchio and Cequea (1998). The genus *Xenomugil*, represented by its type species *X. thoburni*, was not sampled during the present study. Nevertheless, we were able to incorporate the nucleotide sequences of a 300-bp long fragment of the cytochrome b gene from the single *X. thoburni* specimen analyzed by Livi et al. (2011) (S. Livi, pers. comm.), thus allowing the placement of the genus *Xenomugil* within the Mugilidae phylogeny.

The DNA sequences were edited and managed with BIOEDIT version 7.0 (Hall, 1999) and SE-Al version 2.0 (Rambaut, 1996). Sequences were initially aligned using the automatic multiple-alignment program MUSCLE (Edgar, 2004; http://www.ebi.ac.uk/Tools/muscle/index.html), then adjusted manually based on the inferred amino acid translation or the secondary structure of ribosomal DNA, if necessary. Regions where the amount of variation was high due to the resulting alignment containing invalid assertions of homology (e.g., large insertion/deletion segments showing high dissimilarity in sequence length), these were discarded from the phylogenetic analyses.

From the aligned sequences, we compiled two types of data matrices. The first, or “long-sequence” data matrix (Matrix 1), was constructed from the longer sequences of the amplified fragments of the target genes (3,140-4,104 bp in total; 46 individuals; Table 1), aligned and trimmed to form a matrix 3777 bp long. The 46 individuals were selected from 18 (out of the 20) currently recognized Mugilidae genera. It was not possible to obtain the complete sequences for a number of other individuals, in part because of the lower quality of the tissue samples, in part because of budget and time limitations. The second, or mixed-sequence data matrix (Matrix 2), consisted of all available sequence data obtained during this study, i.e. the full or partial sequences (1,927-4,104 bp in total; Table 1) from a total of 257 individuals from 19/20 ingroup genera, in order to best represent the taxonomic diversity at the genus level, and to globally maximize congruence of the whole set of available relevant characters (Hennig, 1966; Kluge, 1989). It is necessary to ensure that the missing characters in the sequences of a proportion of individuals do not affect the accuracy of the phylogeny. The length of the core sequences in Matrix 2 (i.e., characters specified in all taxa) was 1,932 bp for the 3 genes; hence half of the characters (the other 1953 bp of the 3885) had missing data (Table 1). The sequences of 211/257 individuals (82%) had up to 49% missing characters relative to the standard length of the sequences used for Matrix 1. The missing characters were systematically located in the same portions of the genes (i.e., the 5’ end of the 16S, the 3’ end of the COI and the 3’ end of the cyb genes).
Simulations and empirical results indicate that missing data generally do not affect the accuracy of the phylogeny when (1) they are not randomly distributed among taxa; (2) overall branch lengths are not long and/or characters do not evolve rapidly; (3) sufficient informative data are analyzed with appropriate methods such as Bayesian and likelihood analyses in which realistic sequence evolution models are implemented. Excluding characters simply because they contain missing data cells may itself hamper accurate placement (Wiens and Morrill, 2011). As explained in the above, criteria (1)-(3) were met in the present study.

2.2. Phylogenetic analyses

Descriptive statistics for comparing sequences and a χ² test of homogeneity for base frequencies across individuals (conducted for each gene and codon position separately) were performed using PAUP* version 4.0 (Swofford, 2002). Phylogenetic analyses were conducted based on a partitioned maximum-likelihood (ML) method and partitioned Bayesian approach (BA) as implemented in RAxML 7.2.6 (Stamatakis, 2006) and MrBAYES 3.1.1 (Huelsenbeck and Ronquist, 2001), respectively. A mixed model analysis that allows the independent estimation of individual models of nucleotide substitution for each gene partition was used for the analyses. Seven partitions were assigned, which were the 16S ribosomal gene, the first, second, and third positions of the COI gene, and the first, second, and third positions of the cyt b gene. Likelihood-ratio tests (Goldman, 1993), implemented in MRMODELTEST version 2.2 (Nylander, 2004) were used to select best-fit models for each partition in the partitioned Bayesian analysis. Two independent Bayesian searches were conducted for each dataset.

Four independent MCMC chains consisted of 3,000,000 replicates, sampling one tree per 100 replicates. The distribution of log-likelihood scores were examined to determine stationarity for each search and to decide if extra runs were required to achieve convergence in log-likelihoods among runs or searches. Initial trees with non-stationary log-likelihood values were discarded, and the remaining chains of trees resulting in convergent log-likelihood scores from both independent searches were combined. These trees were used to construct a 50% majority rule consensus tree.

For the partitioned ML search with the mixed model of nucleotide substitution, a (GTR+G+I) model (with 4 discrete rate categories) for each partition was used, since RAxML only provides GTR-related models [GTR+G], (GTR+G+I) and (GTR+CAT) approximation of rate heterogeneity for nucleotide data (Stamatakis, 2006). Maximum-likelihood analysis was conducted with 10 separate runs using the default algorithm of the program and with a maximum parsimonious tree as the starting tree for each run. The ML tree was selected among suboptimal trees in each run by comparing likelihood scores under the (GTR+G+I) model. This was repeated 10 times, and the tree with the best likelihood score among 10 ML trees for each analysis was selected as the final tree.

Nodal support was assessed by bootstrapping (Felsenstein, 1985) with the ML criterion, based on 1000 pseudo-replicates and the resulting a posteriori probabilities from partitioned BA. The ML analyses (through analyses using RAxML web-servers) (Stamatakis et al., 2008) were conducted with the CIPRES cluster (CIPRES Portal 1.15; http://www.phylo.org/sub_sections/portal/) at the San Diego Supercomputer Center (San Diego CA, U.S.A.).

Alternative phylogenetic trees were constructed, where the monophyly of each of the genera Agonostomus, Liza, Moolgarda, Myxus, Oedalechilus, Rhinomugil, Sicamugil, and Valamugil was imposed. The likelihood of these alternative hypotheses was tested using the S-H test proposed by Shimodaira and Hasegawa (1999) as implemented in PAUP*. Nine such constrained ML analyses, based on Matrix 1 were performed. The log-likelihood scores obtained using a GTR+G+I model with single partitioning were then compared to the score of the best tree. The significance of differences in log-likelihood was evaluated
using bootstrap resampling. The monophyly of the genus *Chelon* could not be tested as only one *Chelon* species was represented in the Matrix 1 dataset.

2.3. Nomenclature

In this paper, we followed the genus and species nomenclature of Eschmeyer and Fricke (2011).

3. Results

3.1. Characteristics of the sequence data

Matrix 1 consisted of the full sequences of the amplified fragments of three mitochondrial genes of 46 Mugilidae individuals and three outgroups, aligned over 3,777 bp. The length of the nucleotide sequence of the 16S gene ranged from 1,315 to 1,355 bp depending on the individual. Indels were therefore required to align sequences. No indel was present in the aligned COI sequences (1,405 bp) and cyt b sequences (1,045 bp). Of the 3,777 nucleotides sites, 1,834 were variable and 1,534 of the latter were parsimony-informative. Matrix 2 consisted of the sequences of 260 individuals with up to 3,885 nucleotide sites aligned, 1,971 of which were variable and including 1,663 parsimony-informative sites. The length of core sequences (i.e., regions where sequences were present for all individuals) was 550 bp for 16S, 598 bp for COI, and 784 bp for cyt b.

Most of the nucleotide variability occurred at the third codon position in both cyt b and COI gene sequences, where transitions were more frequent than transversions. A saturation plateau was visible at the third codon position (absolute saturation tests; Philippe et al., 1994). Tests of the stationarity of base composition revealed a bias in base composition at the third codon position in the cyt b and COI gene sequences and the analyses based on RY-coded nucleotides were therefore used (Chen and Mayden, 2009). Accordingly, nucleotides at the third codon position in protein-coding genes were coded as purines (R) or pyrimidines (Y) and the phylogenetic tree inferred from the resulting data-matrix was compared to the original phylogeny. There was no significant difference for the higher-level relationships of Mugilidae between the analyses on the RY-coded matrix and those on the original matrix. Therefore, only the results from the original analyses on both Matrices 1 (Fig. 2) and 2 (Figs. 3-5) were presented. The use of RY-coded nucleotides to avoid potential homoplasy might inconveniently result in the loss of useful phylogenetic information, especially in the shallow branches of the tree.

3.2. Inferred phylogenetic trees

The phylogenetic relationships at the genus level and above, as inferred from partitioned ML and Bayesian analyses of Matrices 1 and 2, are presented in Fig. 2 and Fig. 3 respectively. The topologies of the two trees were nearly identical, except for slight differences in relationships where nodal supports were weak. Some of the inferred relationships were strongly supported by bootstrap scores from the ML analysis, and by *a posteriori* probabilities from partitioned Bayesian analysis (Figs. 2 and 3). A clade including *Ellochelon*, *Oedalechilus labiosus* and *Rhinomugil nasutus* and a clade including *Crenimugil crenilabis*, *Moolgarda* spp. and *Valamugil* spp. were found to be sister clades with strong support using partitioned Bayesian analysis but only a weak bootstrap score under maximum-likelihood analysis (Figs. 2 and 3). The statistical support of some deep nodes was improved when Matrix 2 was used. For instance, *Chaenomugil*, *Cestraeus*, *Mugil* and a clade including *Agonostomus* spp. and *Joturus*, formed a monophyletic group sister to...
the clade formed by *Myxus elongatus* and *Neomyxus*, with stronger support for the results inferred from Matrix 2 (Fig. 3) than Matrix 1 (Fig. 2). Similarly, the sister-group relationship between *Liza argentea* and *Aldrichetta* had a higher posterior probability in the Bayesian analysis with Matrix 2 than Matrix 1. This suggests that a denser sampling of taxa, as in Matrix 2 relative to Matrix 1, improves the accuracy of phylogenetic inference (Hillis, 1996). Accordingly, the family was found to comprise 7 major clades that have radiated early from the ancestor to all current Mugilidae (Fig. 3). The phylogenetic relationships among Mugilidae genera, as inferred from the present analyses, are summarized in Fig. 1F.

A detailed account of the phylogenetic placement of each Mugilidae genus is given below, where genera are listed in alphabetical order.

*Agonostomus* was paraplythetic with respect to *Joturus* (Fig. 3); *A. monticola* was phylogenetically closer to *J. richardi* than both were to *A. catalai*. The nucleotide divergence between *A. monticola* and *A. catalai* at locus 16S was 13.3-13.5% [Kimura 2-parameter; MEGA 5; Tamura et al. (2011)] while the estimated divergence between *A. telfairii*, the type-species of the genus (GENBANK DQ532834) and *A. catalai* was 0.2%.

*Aldrichetta* was found to be the sister subclade of *Liza argentea* (Fig. 3).

*Cestraeus*, represented by two species (*G. goldiei* and *C. acryrhinchus*) was found to be monophyletic and a brother genus to *Chaenomugil, Mugil, and (Agonostomus + Joturus)*.

*Chaenomugil* was found to be a brother genus to *Cestraeus, Mugil* and (*Agonostomus + Joturus*).

*Chelon labrosus* grouped with *L. aurata*, *L. ramada*, *L. saliens*, *L. richardiouii*, *L. bandialensis*, *L. dumerilii* and *L. tricuspidens* (Fig. 5A) to form a monophyletic subclade (Fig. 3), which turned out to exclusively comprise species distributed in Atlantic and Mediterranean waters or around southern Africa. The other *Chelon* species sampled, all from the Indo-Pacific, formed a distinct subclade together with Indo-Pacific *Liza* spp. and *Paramugil parmatus* (Fig. 3; Fig. 5A).

*Crenimugil crenilabis* formed a distinct cluster with *Moolgarda sebeli* and *Valamugil buchanani* within the *Crenimugil-Moolgarda-Valamugil* subclade (Fig. 3; Fig. 5B).

The monotypic genus *Ellochelon* was found to be the sister lineage of *Oedalechilus labiosus* (Fig. 3).

We found the monotypic genus *Joturus* to be the sister lineage of *Agonostomus monticola*.

Each *Liza argentea* and *L. falcipinnis* was separate from the other *Liza* species, all of which clustered within a single clade. The latter comprised *Myxus capensis, Oedalechilus laboe*, and three subclades: one that corresponds to *L. grandisquamis*, a second one that includes *Chelon labrosus* and all *Liza* spp. of the Atlantic and the Mediterranean [see (5) above], and a third sub-clade that includes *Chelon* spp. and *Liza* spp. from the Indo-Pacific only (namely, *C. macrolepis, C. melinopterus, C. planiceps, C. subviridis, L. abu, L. affinis, L. alata, L. baematocheila, and Paramugil parmatus*) (Fig. 3 and Fig. 5A).

*Moolgarda* was polyphyletic (Fig. 3).

All 11 *Mugil* species examined here (*M. bahanensis, M. bandialensis, M. capurii, M. cephalus, M. curema, M. buspes, M. incolis, M. liza, M. platanus, M. rubrioculus* and *M. triboodon*) clustered into a single, well-supported clade (Figs. 3-4).

*Myxus* turned out to be polyphyletic, with *M. elongatus* (its type-species) pairing with *Neomyxus leuciscus*, and *M. capensis* being part of the distinct clade external to *O. laboe* and the two (*Liza* spp. + *Chelon* spp.) subclades (Fig. 2).

*Neomyxus* was found to be the sister lineage of *M. elongatus*.

*Oedalechilus* turned out to be polyphyletic: *O. laboe* (the type species) clustered with *Myxus capensis, Chelon* spp., *Liza* spp. and *P. parmatus* to form a distinct subclade, while *O. labiosus* paired with *E. vaigensis* within another subclade that also included *R. nasutus* (Fig. 3; Fig. 5A).

*Paramugil parmatus*, the type-species of the genus, was embedded within the Indo-Pacific sub-clade of (*Liza* spp. + *Chelon* spp.) (Fig. 3).
Rhinomugil was found to be polyphyletic, with R. corsula being the sister lineage of Sicamugil cascasia, while R. nasutus was found to pair with the lineage that includes Ellechelon and O. labiosus (Fig. 3).

Sicamugil was found to be paraphyletic (Fig. 3), where S. hamiltonii was the sister subclade of (R. corsula + S. cascasia).

Genus Traceystoma formed a distinct clade on its own (Fig. 3).

Most Valamugil species, along with Moolgarda species, split into two strongly supported lineages, one of which was paraphyletic with Crenimugil crenilabis (Fig. 5B). V. robustus belonged to another subclade, which also comprised Moolgarda spp. and Valamugil spp.

Xenomugil thoburni was not included in the present phylogenetic analysis, as only a 300-bp long sequence of the cyt b gene of this species was available to us. Maximum-likelihood analysis of the homologous fragment for a sample of species including X. thoburni, all Mugil spp. presented in Fig. 3, and 22 other Mugilidae species (from 16 genera) showed the X. thoburni haplotype embedded within the Mugil curema haplogroup.

In summary, all genera that were represented by two species or more, except Cestraeus, turned out to be paraphyletic or polyphyletic. The results of the S-H test confirmed that Liza, Moolgarda, Myxus, Oedalechilus, Rhinomugil and Valamugil are not monophyletic. The likelihood of trees constrained by the monophyly of Agonostomus and Sicamugil was also lower than that of the unconstrained tree, although not significantly so (Table 3).

3.3. Phylogeny at the infra-generic level

On the mitochondrial tree of species (Figs. 2-5), the two Myxus species split into two independent lineages, as did the two Oedalechilus and the two Rhinomugil species. Agonostomus was paraphyletic with Joturus, as were Moolgarda and Valamugil with Crenimugil. Sicamugil was paraphyletic with Rhinomugil corsula. L. argentea and L. falcipinnis formed independent clades (Fig. 3). Chelon spp., all other Liza spp. and Paramugil parmatus clustered into a distinct subclade, which comprised three lineages: one that corresponds to L. grandisquamis, a second one that includes Indo-Pacific Chelon spp. and Liza spp. together with P. parmatus, and a third lineage that includes Chelon labrosus and all Liza spp. of the Atlantic and the Mediterranean (Figs. 3 and 5A). The other genera analysed here were monophyletic.

3.4. Phylogeny at the infra-specific level

The phylogeographic structures of a number of the Mugilidae species sampled across a wide geographic range are briefly described below.

Agonostomus monticola: all haplotypes sampled were grouped into a single clade consisting of three distinct lineages, two from the Pacific and one from the Atlantic; the Atlantic lineage was the sister lineage of one of the Pacific lineages (Fig. 3).

Chelon macrolepis: two separate haplogroups were present in this monophyletic species; one haplogroup included all haplotypes sampled west of Oman, while the other haplogroup included haplotypes from the Maldives archipelago and east of it.

Crenimugil crenilabis: all haplotypes sampled across the Indo-Pacific formed a single clade with shallow topology; the haplotype sampled in the Seychelles (western Indian Ocean) was identical to the haplotype sampled in the Chesterfield Islands (western Pacific Ocean) (Fig. 5B).

Liza alata: haplotypes of this species formed a paraphyletic haplogroup, with one lineage comprising haplotypes sampled from the Indian Ocean coast of South Africa and a distinct lineage grouping the haplotypes sampled in Australia (Fig. 5A).
Liqa dumerili: two sister lineages were observed; one lineage consisted of all haplotypes from the Indian Ocean coast of South Africa and the other lineage consisted of haplotypes sampled in West Africa (Fig. 5A).

Moolgarda cunnesius: the haplotype sampled in eastern South Africa formed a lineage distinct from that sampled in Taiwan; the latter was a sister lineage to M. cunnesius from Australia and M. perniti from New Caledonia and from Taiwan.

Moolgarda sebeli: the haplotypes of a number of individuals of this species clustered into one of three haplogroups that together formed a clade paraphyletic with Crenimugil crenilabis and with an unidentified Valamugil species sampled from Taiwan and Fiji (Fig. 5B). One M. sebeli haplogroup was sampled in Vietnam and in northern and northeastern Australia; a second haplogroup was present all across the Indo-Pacific, from the Seychelles to Taiwan and Fiji; the third haplogroup, also present across the Indo-Pacific, from the Southwestern Indian Ocean to New Caledonia, was a sister clade of C. crenilabis (Fig. 5B).

Mugil cephalus: the ‘M. cephalus complex’ subclade (Fig. 3) consisted of a rake-like subtree with 14 parallel lineages that included the M. liqo lineage and 13 other lineages, all currently designated as M. cephalus. Generally, each lineage had a regional distribution (Fig. 4A) whereas in some instances, different lineages co-exist at a single locality [e.g., lineages L1-L3 in Taiwan (Fig. 4A); another example is New Caledonia where two lineages were sampled, one of which was also sampled in New Zealand, the other one (L3) also occurring in Fiji and Taiwan].

Mugil curema: haplotypes of this species formed an apparent monophyletic haplogroup, although the node separating M. curema from M. inciliis was not resolved. This ‘M. curema’ haplogroup consisted of at least four lineages, one present exclusively in the eastern Atlantic, two from the western Atlantic, and one sampled on the Pacific coast of North America. One of the two western-Atlantic lineages paired with the eastern-Pacific group and both formed a monophyletic group with the eastern-Atlantic haplotypes (Fig. 4B). Thus, two M. curema lineages were sampled along the tropical Atlantic coast of America; one of these lineages is the ‘Type 2’ of Fraga et al. (2007), which is characterized by 2n=28 chromosomes as confirmed in the present study (Table 1), whereas the specimens karyotyped in the other lineage had 2n=24 (Table 1).

Valamugil buchananii haplotypes sampled from distant locations in the Indo-Pacific formed a single lineage with shallow topology (Fig. 5B).

4. Discussion

4.1. Phylogenetic relationships among Mugilidae genera

The genus rather than the species is currently designated as the analytical unit for a wide range of large-scale analyses in systematics, biogeography and conservation biology (Mandelik et al., 2007; Villaseñor et al., 2005). Consequently, the significance of our results relating to the systematics of Mugilidae is discussed at the genus level.

Previous investigations using various anatomical characters, have provided conflicting hypotheses on the systematic relationships within the family Mugilidae (Ghasemzadeh, 1998; Harrison and Howes, 1991; Schultz, 1946; Senou, 1988; Thomson, 1997; Fig. 1 A-E). The only area of agreement by the above authors is the phylogenetic position of genera Agonostomus and Joturnus. These genera have been positioned as a basal clade in the phylogenies of the family (Schultz, 1946; Senou, 1988; Thomson, 1997) and have been declared “primitive” (Schultz, 1946) or part of a “primitive” sub-family of the Mugilidae (Agonostominae: Thomson, 1997). In contrast, Schultz (1946) considered Cestraeus to be closely related to
Chaenomugil and regarded the latter, together with Neomugil and Xenomugil spp., to be highly specialized (owing to the anatomical features of their lips and teeth). In the present study, Agonostomus (in part) and Joturus were found to be closely related to each other, and formed a monophyletic clade. However, this clade did not branch early in the phylogeny, but appeared as a relatively modern divergence. We agree with Schultz (1946) in placing Cestraeus together with Chaenomugil, but both these genera also clustered with Joturus and Agonostomus. A close relationship between Oedalechilus and Chelon has also been reported by both Schultz (1946) and Thomson (1997); molecular data concur with this finding (Heras et al., 2009; this study).

In order to test the other hypotheses involving relationships among the Mugilidae genera presented in Fig. 1A-E, a fully resolved molecular phylogeny of the entire family would be required. Unfortunately, the deeper nodes of the present mitochondrial phylogenetic tree indicated insufficient resolution to properly address the issue. A salient point is that the present results already indicate that the morpho-anatomy of the mouth is poorly informative from a phylogenetic perspective.

The mitochondrial phylogeny of the Mugilidae was characterized by long terminal branches and short internal branches, reflecting either mutational saturation or rapid radiation occurring during the early diversification of the family. The latter seems most likely given that little difference was visible between the original and the RY-coded analyses. Employing slower-evolved and independent nuclear gene markers might prove helpful to address this issue.

4.2. Implications of the present molecular data to Mugilidae taxonomy at the genus level

Morpho-anatomical taxonomy at the genus level in the Mugilidae is still under debate. For example, Schultz (1946) considered the genus Liza as a junior synonym of Chelon but this view was challenged by Thomson (1997) on the grounds that Liza species all lack the lip ornamentation of Chelon. Thomson’s (1997) recognition of Liza as a distinct genus has in turn been questioned by several authors (reviewed by Heras et al., 2009) but Liza is still currently considered a valid genus (Eschmeyer and Fricke, 2011). Another example of taxonomic confusion is the recent erection of the genus Paramugil to account for the peculiar morphological and osteological characters shared by P. parmatus and P. georgii (Ghasemzadeh, 1998; Ghasemzadeh et al., 2004). The genus Paramugil is apparently not accepted by Nelson (2006), who recognizes only Liza and Valamugil as the genera for these two species, respectively. The genus Plicomugil proposed by Schultz (1953), and retained by Harrison and Howes (1991) and Nelson (2006), has not been recognized as valid by Ghasemzadeh (1998) and is currently considered to be a synonym of Oedalechilus (Eschmeyer and Fricke, 2011). The erection of the genus Osteomugil for Moolgarda cunningus (Lüther, 1982) has also been ignored in subsequent revisions, for example by Thomson (1997), who considers Osteomugil as a junior synonym of Valamugil and Moolgarda as a nomen dubium.

The present results support an in-depth revision of the taxonomy of the Mugilidae at the genus level. All currently-recognized Mugilidae genera are represented by two species or more, except Cestraeus, and turned out to be paraphyletic or polyphyletic. Alternative topologies, where the monophyly of each of the problematic genera was imposed, proved much less likely than the topology of the ML tree (Fig. 2). The mitochondrial phylogeny offered no rationale for distinguishing Moolgarda from Valamugil, and Liza from Chelon, leading us to challenge their validity. The distinction of two other currently accepted genera (Paramugil and Xenomugil) turned out to be unsupported by phylogeny.

4.4. Taxonomic uncertainty at the species level

Mugilidae species occupy inshore habitats. Their populations are expected to comprise discrete adult
subpopulations that exchange migrants through the pelagic larval phase and large stretches of ocean are expected to constitute geographic barriers to dispersal. Nevertheless, several species exhibit broad distribution, e.g. *Mugil cephalus*, which is reputed as one of those rare cases of a littoral marine fish with circumglobal distribution (Briggs, 1960) but whose taxonomic status as a single species has been questioned (Briggs, 1960; Crosetti et al., 1994; Heras et al., 2009). Other species with wide distribution are *M. curema*, which is present on both sides of the tropical Atlantic and on the Pacific shores of tropical America, and several Indo-Pacific species (e.g. *C. crenilabis*).

Our sampling design allowed testing of the null hypothesis of genetic homogeneity in several widespread Mugilidae species. The results indicated apparent genetic homogeneity in the case of *C. crenilabis* and *V. buchanani*. Some geographic structure was uncovered in *Chelon macrolepis*, where all haplotypes sampled east of the Maldives to as far as Fiji were nearly identical and formed a lineage separate from that consisting of all haplotypes sampled west of Oman, thus suggesting the possible existence of a mid-Indian Ocean barrier. Multiple-mitochondrial lineages were present in *Agonostomus monticola*, *Moolgarda sebeli*, *Mugil cephalus* and *M. curema*, thus raising the possibility that each of these species actually consists of several cryptic species as discussed below.

Our results show that *A. monticola* under its current definition harbours three distinct lineages, two of which are sympatric off western Central America. *Moolgarda sebeli* haplotypes grouped into three independent lineages paraphyletic with other species, implying that *M. sebeli* also might well consist of a complex of three species, at least two of which have a wide Indo-Pacific distribution.

A majority of the 14 mitochondrial lineages in the *Mugil cephalus* complex have regional distribution patterns and are allopatric; however, three of these lineages, L1, L2 and L3 (Fig. 4A), occur sympatrically in Taiwan and have been proven to be reproductively isolated species (Shen et al., 2011). The above results suggest that the ‘*M. cephalus* species complex’ may well consist of up to 14 biological species. This species complex already includes *M. cephalus*, which harbours the mitochondrial lineage sampled in Mediterranean waters, the type-locality (Linnaeus, 1758), and *M. liza*. Further taxonomic work will be necessary to assign a name to each of the three lineages in Taiwanese waters. Additional investigations are warranted to address the question of whether the remaining 9 mitochondrial lineages now uncovered in the *Mugil cephalus* complex also consist of separate species.

Four separate lineages were uncovered in *M. curema*, two of which have overlapping distributions off Venezuela. The difference in chromosome number between the two sympatric lineages strongly suggests that they are reproductively isolated. The type locality of *M. curema* (Bahia) is located in Brazil where T2 was the only lineage sampled, leading to the designation of it as the valid *M. curema*. Further taxonomic work will be necessary to assign a name to each of the remaining three lineages.

The remaining species, for which wide geographic samples were obtained, included *Chelon planiceps*, *Liza alata*, *L. dumerili*, and *Moolgarda cunnesius*. In all cases these species showed strong differences between the regions. For each *C. planiceps*, *L. alata* and *M. cunnesius*, the haplotypes sampled in the southwestern Indian Ocean belonged to a lineage distinct from those sampled around Australia, to the extent that also raises the suspicion of cryptic species.

In conclusion, the Mugilidae offer a wide range of genetic compositions for a littoral marine family, ranging from species that are genetically homogeneous at the scale of the Indo-Pacific (*Crenimugil crenilabis*, *V. buchanani* and some of the *Moolgarda* spp. that belong to the same subclade), versus *Mugil cephalus*, once presented as an example of globally distributed species and now shown to harbor several cryptic species. The Mugilidae also comprise species that exhibit all possible other cases between the above two extremes. Clarifying the taxonomy of Mugilidae at the species level will require considerably more research, for which the present phylogeny hopefully will constitute a sound basis.
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References


Table 1

List of Mugilidae individuals sequenced at three mitochondrial DNA loci (16S rRNA, COI, cytb), with identification, sampling details, individual number as utilized in Figs. 2-5, museum collection numbers and GenBank accession numbers. GenBank accession numbers in bold indicate the 'long' sequences used for constructing Matrix 1 (Fig. 2) and concerns 46 individuals sequenced over 3,140 bp to 4,104 bp in total; the total length of the sequences for the remaining 211 individuals ranged from 1,927 bp to 2,131 bp. Identification was done according to Thomson (1997) and Harrison and Senou (1999), and the genus and species names are those currently accepted in Eschmeyer and Fricke (2011). When a species' identification was uncertain, an unknown species or “sp.” was assigned to the recognized genus for the taxon.

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16S rRNA COI cytb
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Moolgarda cunnesius

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J. Paxton
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Moolgarda cunnesius

Don Son Town, Vietnam
22 Mar. 2010
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ASIZP0061397
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JQ060742 JQ060497 JQ060240

Moolgarda seheli

Saipan, Mariana Islands
24 May 2003
K.A. Moores, E. Heemstra, A.C. Bentley, P.C. Heemstra
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KU:KU:32523
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Garapan Lagoon off Oceanside Bar, Saipan, Mariana Island
24 May 2005
K.A. Moores, E. Heemstra, A.C. Bentley, P.C. Heemstra
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KU:KUIT:5647
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Al Khobar, Saudi Arabia, Persian Gulf
Nov.-Dec. 2008
Z. Batang, P. Premal
JQ060756 JQ060511 JQ060254

Moolgarda seheli

Ternay Bay, Seychelles
14 May 2005
P.C. Heemstra, E. Heemstra, M.J. Smale, A.C. Bentley, et. al.
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JQ060758 JQ060513 JQ060256

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JQ060761 EF069494 JQ060259

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South Gooburn Island, NT, Australia
30 Nov. 2004
R. Williams
234
NTM S.16014-002
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JQ060762 JQ060516 JQ060260

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Fish River, Daly River area, NT, Australia
06 Sep. 2001
R. Williams
235
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JQ060763 JQ060517 JQ060261

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19 May 2005
P.C. Heemstra, E. Heemstra, M.J. Smale, A.C. Bentley, et. al.
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JQ060757 JQ060512 JQ060255

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JQ060766 JQ060519 JQ060263

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<td>N. Laurrabaquio Alvarado</td>
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<td>11 Nov. 2008</td>
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<td>16 June 2008</td>
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<td><em>Mycto apertis</em></td>
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<td>29 July 2003</td>
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<td><em>Neomyxus leuciscus</em></td>
<td>Saipan, Marianas Islands</td>
<td>23 Apr. 2003</td>
<td>K.A. Moorts, E. Heemstra</td>
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<td>Apr. 2003</td>
<td>H. Bles</td>
<td>JQ060837, JQ060836, JQ060835, JQ060834</td>
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<td><em>Paramugil parvatus</em></td>
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<td>July 2008</td>
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<td>JQ060836, JQ060835, JQ060834, JQ060833</td>
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<td>15 Aug. 2004</td>
<td>P.-F. Lee</td>
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AMS: Australian Museum, Sydney
ASIZP: Museum of Institute of Zoology, Academia Sinica, Taipei
CRIMP: Centre for Research into Introduced Marine Pests, Townsville
CSIRO: Commonwealth Scientific and Industrial Research Organisation, Hobart
DIFS: Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown
FNHM: Florida Natural History Museum, St Louis
KU: Natural History Museum & Biodiversity Research Center, Lawrence
MNHN: Museum national d’histoire naturelle, Paris
NMMBP: National Museum of Marine Biology, Keelung
NMNS: National Museum of Nature and Science, Tokyo
NMV: Museum Victoria, Melbourne
NRM: Swedish Museum of Natural History, Stockholm
NTM: Museums and Art Galleries of the Northern Territory, Darwin
SAIAB: South African Institute of Aquatic Biology, Grahamstown
STRI: Smithsonian Tropical Institute, Panama
UABC: Universidad Autonoma de Baja California, Tijuana
UDOV: Universidad de Oriente Venezuela, Porlamar
USMI: University of Southern Mississippi Ichthyology Collection, Hattiesburg

(a) 16S rRNA and Cytb gene sequences identical to those of MNHN 2009-0806
(b) karyotype: 2n = 24 chromosomes
(c) karyotype: 2n = 28 chromosomes
(d) karyotype: 2n = 48 chromosomes
(e) 16S rRNA and Cytb gene sequences identical to those of MNHN 2009-0809
Table 2
Primer names used for the PCR amplification and sequencing of mitochondrial *16S*, *COI*, and *cyt b* gene fragments in Mugilidae.

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<td>16S-ARL</td>
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<td>Palumbi et al. (1991)</td>
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<td>Palumbi et al. (1991)</td>
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<td>FishF1</td>
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<td>Ward et al. (2005)</td>
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<td><strong>cyt b</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FishcytB-F</td>
<td>5′−ACCACCGTTTATTTCAACTACAAGAC−3′</td>
<td>52°C</td>
<td>Sevilla et al. (2007)</td>
</tr>
<tr>
<td>GlmA 1F</td>
<td>5′−GGCTTGAACCAACCCGTTG−3′</td>
<td>52°C</td>
<td>present study</td>
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<tr>
<td>Cytob610-F</td>
<td>5′−GAAAAACCGCTCAYAAYACCC−3′</td>
<td>52°C</td>
<td>present study</td>
</tr>
<tr>
<td>MixCytob937-2R</td>
<td>5′−GKGCGGAATGTYAGGTTTG−3′</td>
<td>52°C</td>
<td>present study</td>
</tr>
<tr>
<td>TraceyB-R</td>
<td>5′−CCGACTTCCGAGATACAGACC−3′</td>
<td>52°C</td>
<td>Sevilla et al. (2007)</td>
</tr>
</tbody>
</table>
Table 3

Results of Shimodaira and Hasegawa’s (1999) S-H tests of alternative phylogenetic hypotheses, where each genus in turn is assumed to be monophyletic. Log (ln)-likelihood difference to the best ML tree (Δ) and associated probability (P; from 10,000 pseudo-samples generated by bootstrap)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Δ</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sicamugil</td>
<td>0.3</td>
<td>0.985</td>
</tr>
<tr>
<td>Agonostomus</td>
<td>4.6</td>
<td>0.944</td>
</tr>
<tr>
<td>Rhinomugil</td>
<td>108.5</td>
<td>&lt; 0.008</td>
</tr>
<tr>
<td>Valamugil</td>
<td>145.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Myxus</td>
<td>191.0</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Oedalechilus</td>
<td>252.9</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Liza</td>
<td>284.7</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Moolgarda</td>
<td>550.4</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
Captions to Figures

Fig. 1. Previous and current hypotheses of the phylogenetic relationships among Mugilidae genera based on morpho-anatomy (A-E) and mitochondrial DNA sequences (F). (A) Tree in Schultz (1946). (B) Phylogeny of genera according to Senou (1988). (C) Tree in Harrison and Howes (1991). (D) Tree reconstructed after Thomson (1997). (E) Phylogeny of Indo-Pacific Mugilidae genera according to Ghasemzadeh (1998). (F) Present study; asterisks flag genera which were found to be polyphyletic or paraphyletic. Grey brackets on the right of the figure indicate the 7 major clades uncovered by the phylogenetic analysis.

Fig. 2. Phylogenetic tree depicting relationships among major lineages within the Mugilidae. Relationships were inferred using partitioned maximum-likelihood (ML) analysis of 3,777 aligned nucleotides from three mitochondrial gene loci based on data Matrix 1 (complete sequences). ML score of the tree is -53312.03. Branch lengths are proportional to the number of substitutions under the (GTR+G+I) model. Numbers on the branches are ML bootstrap values, with those below 50% not shown. Asterisks indicate nodes with a posteriori probability from partitioned Bayesian analysis ≥ 0.95. Genus and species names follow Eschmeyer and Fricke (2011). When species identification was uncertain, an unknown species or “sp.” was assigned to the recognized genus for the taxon. Scale bar: 0.2 inferred nucleotide substitution/site under the (GTR+G+I) model.

Fig. 3. Phylogenetic tree depicting relationships among 55 currently-recognized Mugilidae species (Eschmeyer and Fricke, 2011). Relationships were inferred using partitioned maximum-likelihood (ML) analysis of 3,885 aligned nucleotides from three mitochondrial gene loci based on data Matrix 2 (or mixed sequence data matrix). ln(L) score of the tree was -70948.2. Branch length is proportional to the number of substitutions under the (GTR+G+I) model. Numbers on the branches are ML bootstrap values (in %, from 1000 replicates), with those below 50% not shown. Asterisks indicate nodes with a posteriori probability from partitioned Bayesian analysis of ≥ 0.95. When species identification was uncertain, an unknown species or “sp.” was assigned to the recognized genus for the taxon. Relationships for the species from the Mugil curema complex and the Mugil cephalus complex are shown in Fig. 4A and B, and those for the genera Chelon, Liza and Paramugil, as well as Moolgarda and Valamugil, are shown in Fig. 5A and B respectively. The branch leading to the most derived sequence in each of these complexes reaches the vertical side at the right of the triangle. Scale bar: 0.1 inferred nucleotide substitution/site under (GTR+G+I) model. NC: New Caledonia. Darker-grey background: genus name in need of revision; lighter grey: genus monophyletic.

Fig. 4. Detail of two subclades from the phylogenetic tree of the Mugilidae presented in Fig. 3. (A) Mugil cephalus complex; L1, L2 and L3 are, respectively, lineages 1, 2 and 3 of Shen et al. (2011). (B) Mugil curema complex, including M. incilis; T2 is Type 2 of Fraga et al. (2007). Scale bar: number of inferred nucleotide substitutions/site under (GTR+G+I) model. NC: New Caledonia.

Fig. 5. Detail of the speciose branches from the phylogenetic tree of the Mugilidae, as presented in Fig. 3. (A) Genera Chelon, Liza and Paramugil. (B) Genera Crenimugil, Moolgarda and Valamugil. NC: New Caledonia.
Fig. 4 - Durand et al.
Fig. 5 - Durand et al.