



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

Jean-Dominique Durand, Kang-Ning Shen, Wei-Jen Chen, Brian W. Jamandre, Hager Blel, K. Diop, Mauricio Nirchio, Francisco Javier Garcia de Leon, Alan K. Whitfield, Chih-Wei Chang, et al.

► To cite this version:

Jean-Dominique Durand, Kang-Ning Shen, Wei-Jen Chen, Brian W. Jamandre, Hager Blel, et al.. Systematics of the grey mullets (Teleostei: Mugiliformes: Mugilidae): molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy. *Molecular Phylogenetics and Evolution*, 2012, 64, pp.73-92. ird-00695484

HAL Id: ird-00695484

<https://ird.hal.science/ird-00695484>

Submitted on 8 May 2012

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

To be cited as:

DURAND J.-D., SHEN K.-N., CHEN W.-J., JAMANDRE B.W., BLEL H., DIOP K., NIRCHIO M., GARCÍA DE LEÓN F.J., WHITFIELD A.K., CHANG C.-W., BORSA P. 2012. – Systematics of the grey mullets (Teleostei: Mugiliformes: Mugilidae): Molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy. *Molecular Phylogenetics and Evolution* 64, 73-92.

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

J.-D. Durand ^{a*}, K.-N. Shen ^b, W.-J. Chen ^c, B.-W. Jamandre ^b, H. Blel ^d, K. Diop ^a, M. Nirchio ^e, F.J. Garcia de León ^f, A.K. Whitfield ^g, C.-W. Chang ^h, P. Borsa ⁱ

^a Institut de recherche pour le développement (IRD), UMR5119 ECOSYM, Bat.24 Cc.093, Université Montpellier 2, Place E. Bataillon 34095, Montpellier cedex 5, France

^b Institute of Fisheries Science, National Taiwan University, No.1, Sec. 4, Roosevelt Rd., Taipei 10617, Taiwan

^c Institute of Oceanography, National Taiwan University, No.1 Sec. 4 Roosevelt Rd. Taipei 10617, Taiwan

^d Unité de recherche de génétique: Biodiversité et valorisation des bio ressources (UR 09/30), Institut supérieur de biotechnologie de Monastir, Monastir, Tunisie

^e Escuela de Ciencias Aplicadas del Mar, Universidad de Oriente, Apartado Postal 147-Portlamar, Isla de Margarita, Venezuela

^f Laboratorio de Genética para la Conservación Centro de Investigaciones Biológicas del Noroeste, S.C. Mar Bermejo No. 195, Col. Playa Palo de Santa Rita La Paz, BCS 23090, México

^g South African Institute for Aquatic Biodiversity, Private Bag 1015 / Somerset Street, Grahamstown 6140, South Africa

^h National Museum of Marine Biology and Aquarium, 2 Houwan Road, Checheng, Pingtung, 944, Taiwan

ⁱ IRD, UR 227 CoReUs, Montpellier, France

* Corresponding author: email: jean-dominique.durand@ird.fr; Tel: +33 4 6714 4571; Fax: + 33 4 6714 3719

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 sebeli*, *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; Blel 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 *cytb*) 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. seбели*, *Mugil cephalus*, *M. curema* and *Valamugil buechanani*.

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 *Abudefduf vaigiensis* (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*, *Chelon macrolepis*, *Crenimugil crenilabis*, *Liza alata*, *L. dumerili*, *Moolgarda cunnesius*, *M. sebeli*, *Mugil cephalus*, *M. curema* and *Valamugil buehanani* (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 oxidase I gene (*COI*), and cytochrome *b* gene (*cytb*) 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 *cytb*) 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 *cytb* 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 χ^2 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 *cytb* sequences (1,045 bp). Of the 3,777 nucleotide 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 *cytb*.

Most of the nucleotide variability occurred at the third codon position in both *cytb* 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 *cytb* 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 *Ellocheilus*, *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 paraphyletic with respect to *Joturus* (Fig. 3); *A. monticola* was phylogenetically closer to *J. pichardi* 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 (*C. goldiei* and *C. oxyrinchus*) 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. richardsonii*, *L. bandialensis*, *L. dumerili* 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 parmatius* (Fig. 3; Fig. 5A).

Crenimugil crenilabis formed a distinct cluster with *Moolgarda sebeli* and *Valamugil buehanani* 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 labeo*, 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. haematocheila*, and *Paramugil parmatius*) (Fig. 3 and Fig. 5A).

Moolgarda was polyphyletic (Fig. 3).

All 11 *Mugil* species examined here (*M. bananensis*, *M. bandialensis*, *M. capurii*, *M. cephalus*, *M. curema*, *M. hospes*, *M. incilis*, *M. liza*, *M. platanus*, *M. rubrioculus* and *M. trichodon*) 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. labeo* 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. labeo* (the type species) clustered with *Myxus capensis*, *Chelon* spp., *Liza* spp. and *P. parmatius* to form a distinct subclade, while *O. labiosus* paired with *E. vaigiensis* within another subclade that also included *R. nasutus* (Fig. 3; Fig. 5A).

Paramugil parmatius, 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 *Ellochelon* 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 *Trachystoma* 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 *cytb* 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 parmatius* 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. parmatius*, 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).

Liza 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. perusii* 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. liza* 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. incilis* 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 bichanani: 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 *Joturus*. 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. parmatius* 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 cunnesius* (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. crenilabris*).

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. crenilabris* and *V. buchmanii*. 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 crenilabris*, *V. buchmanii* 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.

Acknowledgements

We thank the numerous people who contributed mugilid samples for this study, namely H. Ashanti, Z. Batang, P. Bearez, A. Bentley, Y. Bettarel, J. Boubée, D.J. Bray, R. Causse, S. Chow, K.W. Conway, P. Cowley, M.T. Craig, I. de Buron, B. Dellling, P. Durville, I. Faye, M. Gomon, B. Gourène, A. Graham, C.-C. Hsu, N. Hubert, S. Kleinertz (SPICE II project), B. Kreiser, S. Kullander, S. Lamberth, P. Laleye, H.K. Larson, R. Lessa, M. Louis, H. Masski, R. Mayden, M. McGrouther, M. Mwale, X.-P. Nie, H. Nouri, D.W. Nyingi, T.K. Ogawa, H. Palm, R. Paperno, A. Pariselle, S. Planes, P. Premlal, P. Pruvost, J. Raffray, B. Roumillat, K. Rowling, O. Sadio, S. Sirvas Cornejo, A. Stein, J.-F. Trape, E. Ünlü, R. Vigouroux, D. Vo, R.D. Ward, and fishermen and fish vendors at the Noumea fish market (P. Morlet, L. Olonde and E. Perronet). Samples were also obtained through the EWiN expedition (LIPI-P2O, Indonesia) to West Papua, with the help of M. Adrim, D.A. Nugroho and the villagers of Rauki; through the project “Biodiversité des Iles de l’Océan Indien: Maldives” (AIRD-IFB, France; S. Andréfouët) with the help of S. Andréfouët, L. Scott, the Maldives Marine Research Center and fishermen from Eydhafushi; through the MUGIL program (INCO-DEV-SSA-1); and through the MULTRACE program (ORCHID 2011 of the National Science Council of Taiwan (NSC 100-2911-I-291-501-MY2) and the French Ministry of the Foreign Affairs). We thank S. Livi for kindly providing the 300-bp cytochrome-b gene sequence in *Xenomugil thoburni*. We thank P. Bearez, W.N. Eschmeyer and R. Fricke for help in sorting out some nomenclatural problems. We are grateful to E.R.A. Durand for writing computer routines to assist with data analysis and presentation, and to two anonymous reviewers for helpful suggestions. This study was funded by IRD-UR 070, UMR5119, UR 128 and UR 227. W.-J. Chen received grant support (NSC 99-2611-M-002-001-MY2) from the National Science Council of Taiwan.

References

- Aurelle, D., Barthelemy, R.-M., Quignard, J.-P., Trabelsi, M., Faure, E., 2008. Molecular phylogeny of Mugilidae (Teleostei: Perciformes). *Open Mar. Biol. J.* 2, 29-37.
- Autem, M., Bonhomme, F., 1980. Eléments de systématique biochimique chez les Mugilidés de Méditerranée. *Biochem. Syst. Ecol.* 8, 305-308.
- Avice, J.C., 2000. *Phylogeography: the history and formation of species*. Harvard Univ. Press, Cambridge, MA. 447 pp.
- Blel, H., Chatti, N., Besbes, R., Farjallah, S., Elouaer, A., Guerbej, H., Said, K., 2008. Phylogenetic relationships in grey mullets (Mugilidae) in a Tunisian lagoon. *Aquaculture Res.* 39, 268-275.
- Briggs, J.C., 1960. Fishes of worldwide (circumtropical) distribution. *Copeia* 1960, 171-180.
- Caldara, F., Bargelloni, L., Ostellari, L., Penzo, E., Colombo, L., Patarnello, T., 1996. Molecular phylogeny of grey mullets based on mitochondrial DNA sequence analysis: evidence of a differential rate of evolution at the intrafamily level. *Mol. Phylogenet. Evol.* 6, 416-424.
- Chen, W.-J., Bonillo, C., Lecointre, G., 2003. Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of acanthomorph (teleostei) with larger number of taxa. *Mol. Phylogenet. Evol.* 26, 262-288.
- Chen, W.-J., Mayden, R.L., 2009. Molecular systematics of the Cyprinoidea (Teleostei: Cypriniformes), the world's largest clade of freshwater fishes: further evidence from six nuclear genes. *Mol. Phylogenet. Evol.* 52, 544-549.
- Chen, W.-J., Mayden, R.L., 2010. A phylogenomic perspective on the new era of ichthyology. *BioScience* 60, 421-432.
- Chen, W.-J., Ruiz-Carus, R., Ortí, G., 2007. Relationships among four genera of mojarras (Teleostei: Perciformes: Gerreidae) from the western Atlantic and their tentative placement among percomorph fishes. *J. Fish Biol.* 70 202-218.

- Crosetti, D., Avise, J.C., Placidi, F., Rossi, A.R., Sola, L., 1993. Geographic variability in the grey mullet *Mugil cephalus*: preliminary results of mtDNA and chromosome analyses. *Aquaculture* 111, 95-101.
- Crosetti, D., Nelson, W.S., Avise, J., 1994. Pronounced genetic structure of mitochondrial DNA among populations of the circumglobally distributed grey mullet (*Mugil cephalus* Linnaeus). *J. Fish Biol.* 44, 47-58.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucl. Acids Res.* 32, 1792-1797.
- Erguden, D., Gurlek, M., Yaglioglu, D., Turan, C., 2010. Genetic identification and taxonomic relationship of Mediterranean mugilid species based on mitochondrial 16S rDNA sequence data. *J. Anim. Vet. Adv.* 9, 336-341.
- Eschmeyer, W. N., Fricke, R., (eds.) 2011. Catalog of fishes, electronic version (<http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>; 5 May 2011).
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783-791.
- Fraga, E., Schneider, H., Nirchio, M., Santa-Brigida, E., Rodrigues-Filho, L.F., Sampaio, I., 2007. Molecular phylogenetic analyses of mullets (Mugilidae, Mugiliformes) based on two mitochondrial genes. *J. Appl. Ichthyol.* 23, 598-604.
- Ghasemzadeh, J., 1998. Phylogeny and Systematics of Indo-Pacific mullets (Teleostei: Mugilidae) with special reference to the mullets of Australia. Ph. D. dissertation. Macquarie University, Sydney, 397 pp.
- Ghasemzadeh, J., Ivantsoff, W., Aarn, 2004. Historical overview of mugilid systematics, with descriptions of *Paramugil* (Teleostei: Mugiliformes: Mugilidae), new genus. *Aqua, J. Ichthyol. Aquat. Biol.* 8, 9-22.
- Goldman, N., 1993. Statistical tests of models of DNA substitution. *J. Mol. Evol.* 36, 182-198.
- Gornung, E., Colangelo, P., Annesi, F., 2007. 5S ribosomal RNA genes in six species of Mediterranean grey mullets: genomic organization and phylogenetic inference. *Genome* 50, 787-795.
- Hall, T.A., 1999. BIOEDIT: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. *Nucl. Acids Symp. Ser.* 41, 95-98.
- Harrison, I.J., Howes, G.J., 1991. The pharyngobranchial organ of mugilid fishes; its structure, variability, ontogeny, possible fonction and taxonomic utility. *Bull. Brit. Mus. Nat. Hist., Zool.* 57, 111-132.
- Harrison, I.J., Nirchio, M., Oliveira, C., Ron, E., Gaviria, J., 2007. A new species of mullet (Teleostei: Mugilidae) from Venezuela, with a discussion on the taxonomy of *Mugil gaimardianus*. *J. Fish Biol.* 71, 76-97.
- Harrison, I.J., Senou, H., 1999. Mugilidae. In: Carpenter, K.E. and Niem, V.H. (eds.), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific, vol. 4: bony fishes part 2 (Mugilidae to Carangidae)*. FAO, Rome, pp. 2069-2108.
- Hennig, W., 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana IL.
- Heras, S., Gonzalez Castro, M., Roldan, M.I., 2006. *Mugil curema* in Argentinean waters: Combined morphological and molecular approach. *Aquaculture* 261: 473-478.
- Heras, S., Roldán, M.I., Gonzalez Castro, M., 2009. Molecular phylogeny of Mugilidae fishes revised. *Rev. Fish Biol. Fisheries* 19, 217-231.
- Hillis, D.M., 1996. Inferring complex phylogenies. *Nature* 383, 130-131.
- Hillis, D.M., 1998. Taxonomic sampling, phylogenetic accuracy, and investigator bias. *Syst. Biol.* 47, 3-8.
- Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES. Bayesian inference of phylogeny. *Bioinformatics* 17, 754-755.
- Imsiridou, A., Minos, G., Katsares, V., Karaiskou, N., Tsiora, A., 2007. Genetic identification and phylogenetic inferences in different Mugilidae species using 5S rDNA markers. *Aquaculture Res.* 38, 1370-1379.
- Jamandre, B.W., Durand, J.-D., Tzeng, W.-N., 2009. Phylogeography of the flathead mullet *Mugil cephalus* in the Northwest Pacific inferred from the mtDNA control region. *J. Fish Biol.* 75, 393-407.
- Ke, H.M., Lin, W.W., Kao, H.W., 2009. Genetic diversity and differentiation of grey mullet (*Mugil cephalus*) in the coastal waters of Taiwan. *Zool. Sci.* 26, 421-428.
- Kluge, A.G., 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38, 7-25.

- Lee, S.C., Chang, J.T., Tsu, Y.Y., 1995. Genetic relationships of four Taiwan mullets (Pisces: Perciformes: Mugilidae). *J. Fish Biol.* 46, 159-162.
- Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M., Lecointre, G., 2009. RNF213, a new nuclear marker for acanthomorph phylogeny. *Mol. Phylogenet. Evol.* 50, 345-363.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I, editio decima, reformata. Holmiae, Stockholm, ii+824 pp.
- Liu, J.-Y., Brown, C.L., Yang, T.-B., 2009. Population genetic structure and historical demography of grey mullet, *Mugil cephalus*, along the coast of China, inferred by analysis of the mitochondrial control region. *Biochem. Syst. Ecol.* 37, 556-566.
- Liu, J.Y., Brown, C.L., Yang, T.B., 2010. Phylogenetic relationships of mullets (Mugilidae) in China Seas based on partial sequences of two mitochondrial genes. *Biochem. Syst. Ecol.* 38, 647-655.
- Livi, S., Sola, L., Crosetti, D., 2011. Phylogeographic relationships among worldwide populations of the cosmopolitan marine species, the striped gray mullet (*Mugil cephalus*), investigated by partial cytochrome *b* gene sequences. *Biochem. Syst. Ecol.* 39, 121-131.
- Lüther, G., 1982. New characters for consideration in the taxonomy appraisal of grey mullets. *J. Mar. Biol. Ass. India* 169, 1-9.
- Mabuchi, K., Miya, M., Azuma, Y., Nishida, M., 2007. Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. *BMC Evol. Biol.* 7, 10.
- Mandelik, Y., Dayan, T., Chikatunov, V., Kravchenko, V., 2007. Reliability of a higher-taxon approach to richness, rarity, and composition assessments at the local scale. *Conserv. Biol.* 21, 1506-1515.
- Menezes, M.R.; Martin, M., Naik, S. 1992. Interspecific genetic divergence in grey mullets from the Goa region. *Aquaculture* 105, 117-129.
- Miya, M., Takeshima, H., Endo, H., Ishiguro, N.B., Inoue, J.G., Mukai, T., Satoh, T.P., Yamaguchi, M., Kawaguchi, A., Mabuchi, K., Shirai, S.M., Nishida, M., 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 26, 121-138.
- Murgia, R., Tola, G., Archer, S.N., Vallerger, S., Hirano, J., 2002. Genetic identification of grey mullet species (Mugilidae) by analysis of mitochondrial DNA sequence: application to identify the origin of processed ovary products (bottarga). *Mar. Biotechnol.* 4, 119-126.
- Nelson, J.S., 2006. *Fishes of the World*. John Wiley and Sons, New York.
- Nirchio, M., Cequea, H., 1998. Karyology of *Mugil liza* and *M. curema* from Venezuela. *Bol. Invest. Mar. Cost.* 27, 45-50.
- Nylander, J.A.A., 2004. MRMODELTEST v. 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.
- Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L., Grabowski, G., 1991. The simple fool's guide to PCR, version 2.0. Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, Honolulu, 47 pp.
- Papasotiropoulos, V., Klossa-Kilia, E., Alahiotis, S., Kiliass, G., 2007. Molecular phylogeny of grey mullets (Teleostei: Mugilidae) in Greece: evidence from sequence analysis of mtDNA segments. *Biochem. Genet.* 45, 623-636.
- Papasotiropoulos, V., Klossa-Kilia, E., Kiliass, G., Alahiotis, S., 2001. Genetic divergence and phylogenetic relationships in grey mullets (Teleostei: Mugilidae) using allozyme data. *Biochem. Genet.* 39, 155-168.
- Papasotiropoulos, V., Klossa-Kilia, E., Kiliass, G., Alahiotis, S., 2002. Genetic divergence and phylogenetic relationships in grey mullets (Teleostei: Mugilidae) based on PCR RFLP analysis of mtDNA segments. *Biochem. Genet.* 40, 71-86.
- Philippe, H., Chenuil, A., Adoutte, A., 1994. Can the Cambrian explosion be inferred through molecular phylogeny? *Development Suppl.* S, 15-25.
- Rambaut, A., 1996. Se-Al: Sequence Alignment Editor ver. 2.0. (Program distributed by the author, Department of Zoology, University of Oxford, Oxford; available online from: <http://tree.bio.ed.ac.uk/software/seal/>).
- Rocha-Olivares, A., Garber, N.M., Stuck, K.C., 2000. High genetic diversity, large inter-oceanic divergence and historical demography of the striped mullet. *J. Fish Biol.* 57, 1134-1149.
- Rossi, A.R., Capula, M., Crosetti, D., Campion, D.E., Sola, L., 1998a. Genetic divergence and phylogenetic inferences in five species of Mugilidae (Pisces: Perciformes). *Mar. Biol.* 131, 213-218.

- Rossi, A.R., Capula, M., Crosetti, D., Sola, L., Campton, D.E., 1998b. Allozyme variation in global populations of striped mullet, *Mugil cephalus* (Pisces: Mugilidae). Mar. Biol. 131, 203-212.
- Rossi, A.R., Ungaro, A., De Innocentiis, S., Crosetti, D., Sola, L., 2004. Phylogenetic analysis of mediterranean Mugilids by allozymes and 16S mt-rRNA genes investigation: are the Mediterranean species of *Liza* monophyletic? Biochem. Genet. 42, 301-315.
- Sambrook, J., Fritschi, E.F., Maniatis, T., 1989. Molecular cloning: a laboratory manual, 2nd edn. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- Schultz, L.P., 1946. A revision of the genera of mullets, fishes of the family Mugilidae, with descriptions of three new genera. Proc. U.S. Natl. Mus. 96, 377-395.
- Schultz, L.P., 1953. Family Mugilidae. In Schultz, L.P., E. S. Herald, E. A. Lachner, A. D. Welander, and L. P. Woods (Ed.) Fishes of the Marshall and Marianas islands, Vol I: Families from Asymmetriontidae through Siganidae. Bull. U.S. Natl Mus. 202, 310-322.
- Semina, A.V., Polyakova, N.E., Makhotkin, M.A., Brykov, V.A., 2007. Mitochondrial DNA divergence and phylogenetic relationships in mullets (Pisces: Mugilidae) of the Sea of Japan and the Sea of Azov revealed by PCR-RFLP-analysis. Russ. J. Mar. Biol. 33, 187-192.
- Senou, H., 1988. Phylogenetic interrelationships of the Mulletts (Pisces: Mugilidae). Ph. D. dissertation. Tokyo University, Tokyo.
- Setiamarga, D.H.E., Miya, M., Yamanoue, Y., Mabuchi, K., Satoh, T.P., Inoue, J.G., Nishida, M., 2008. Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes, silversides, and their relatives): the first evidence based on whole mitogenome sequences. Mol. Phylogenet. Evol. 49, 598-605.
- Sevilla, R.G., Diez, A., Noren, M., Mouchel, O., Jerome, M., Verrez-Bagnis, V., Van Pelt, H., Favre-Krey, L., Krey, G., Bautista, J.M., 2007. Primers and polymerase chain reaction conditions for DNA barcoding teleost fish based on the mitochondrial cytochrome *b* and nuclear rhodopsin genes. Mol. Ecol. Notes 7, 730-734.
- Shen, K.-N., Jamandre, B.W., Hsu, C.-C., Tzeng, W.-N., Durand, J.-D., 2011. Plio-Pleistocene sea level and temperature fluctuations in the northwestern Pacific promoted speciation in the globally-distributed flathead mullet *Mugil cephalus*. BMC Evol. Biol. 11, 83.
- Shimodaira, H., Hasegawa, M., 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol. 16, 1114-1116.
- Smith, W.L., Craig, M.T., 2007. Casting the percomorph net widely: The importance of broad taxonomic sampling in the search for the placement of serranid and percoid fishes. Copeia 2007, 35-55.
- Smith, W.L., Wheeler, W.C., 2006. Venom evolution widespread in fishes: A phylogenetic road map for the bioprospecting of piscine venoms. J. Hered. 97, 206-217.
- Stamatakis, A., 2006. RAxML-VI-HP: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688-2690.
- Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web-servers. Syst. Biol. 57, 758-771.
- Stiassny, M.L.J., 1993. What are grey mullets? Bull. Mar. Sci. 52, 197-219.
- Swofford, D.L., 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer Associates, Sunderland, MA.
- Tamura, K., Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10, 512-526.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA 5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. 28, 2731-2739.
- Thomson, J.M., 1954. The Mugilidae of Australia and adjacent seas. Austr. J. Mar. Freshw. Res. 5, 70-131.
- Thomson, J.M., 1966. The grey mullets. Oceanogr. Mar. Biol. Annu. Rev. 4, 301-355.
- Thomson, J.M., 1997. The Mugilidae of the world. Mem. Queensl. Mus. 43, 457-562.
- Turan, C., Caliskan, M., Kucuktas, H., 2005. Phylogenetic relationships of nine mullet species (Mugilidae) in the Mediterranean Sea. Hydrobiologia 532, 45-51.

- Villaseñor, J.L., Ibarra-Manriquez, G., Meave, J.A., Ortiz, E., 2005. Higher taxa as surrogates of plant biodiversity in a megadiverse country. *Conserv. Biol.* 19, 232-238.
- Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R., Hebert, P.D.N., 2005. DNA barcoding Australia's fish species. *Philos. Trans. R. Soc. Lond. B* 360, 1847-1857.
- Wiens, J.J., Morrill, M.C., 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Syst. Biol.* 60, 719-731.
- Zemlak, T.S., Ward, R.D., Connell, A.D., Holmes, B.H., Hebert, P.D.N., 2009. DNA barcoding reveals overlooked marine fishes. *Mol. Ecol. Resour.* 9, 237-242.

Table 1

List of Mugilidae individuals sequenced at three mitochondrial DNA loci (16S rRNA, COI, cyt b), 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.

Species	Sampling location	Date	Collector(s)	Ind. no.	Voucher no.	Tissue no.	GenBank nos.		
							16S rRNA	COI	cyt <i>b</i>
<i>Agonostomus catalai</i>	Koundré River, Anjouan, Comores	03 Nov. 2005	P. Keith, G. Marquet	023	MNHN 2006-0614	-	JQ060643	JQ060394	JQ060138
<i>Agonostomus monticola</i>	Río Presidio, Sinaloa, Mexico	13 Sep. 2008	S. Sánchez, G. Ruiz, A. Herrera	026	UABC-2052	SGH130908-1	JQ060645	JQ060395	JQ060139
<i>Agonostomus monticola</i>	Río Jiboa, El Salvador	22 Feb. 2006	S. Kullander	028	NRM 53460	-	JQ060646	JQ060396	JQ060140
<i>Agonostomus monticola</i>	Río El Zonte, El Salvador	25 Feb. 2006	S. Kullander	030	NRM 53520	-	JQ060647	JQ060397	JQ060141
<i>Agonostomus monticola</i>	Changuinola River, Boca del Toro, Panama	15 Apr. 2005	M. Nirchio	032	UDOV 314	-	JQ060648	JQ060401	JQ060145
<i>Agonostomus monticola</i>	Bourceau, Guadeloupe	Jan.-Apr. 2008	M. Louis	033	-	-	JQ060652	JQ060402	JQ060146
<i>Agonostomus monticola</i>	La Trilla River, Aragua State, Venezuela	09 May 2007	M. Nirchio	031a	UDOV 700	-	JQ060649	JQ060398	JQ060142
<i>Agonostomus monticola</i>	La Trilla River, Aragua State, Venezuela	-	M. Nirchio	031b	STRI 21827	-	JQ060650	JQ060399	JQ060143
<i>Agonostomus monticola</i>	Guanaja Isld., Honduras	30 June 2005	W.A. Matamoros	031c	-	-	JQ060651	JQ060400	JQ060144
<i>Agonostomus monticola</i>	Río Presidio, Sinaloa, Mexico	13 Sep. 2008	S. Sánchez, G. Ruiz, A. Herrera	035	UABC-2052	SGH130908-2	JQ060644	JQ060403	JQ060147
<i>Aldrichetta forsteri</i>	unknown location, Australia	03 May 1995	G. Yearsley	004	CSIRO H3962-06	-	JQ060653	EF609279	JQ060148
<i>Aldrichetta forsteri</i>	Tauvanga Harbor, New Zeland	10 Oct. 2006	J. Boubee	010	-	-	JQ060654	JQ060405	JQ072905
<i>Cestraeus oxyrhynchus</i>	Trou Bleu River, New Caledonia	24 May 2007	C. Pöllabauer	011	-	-	JQ060656	JQ060407	JQ060150
<i>Cestraeus goldiei</i>	Cagayan Province, Philippines	01 June 2008	B.W. Jamandre	012	-	-	JQ060655	JQ060406	JQ060149
<i>Chaenomugil proboscideus</i>	Los Cerritos, Mexico	18 Apr. 2007	A. Ramirez	002	UABC-1838	AR-CE-0407 46 CP	JQ060657	JQ060408	JQ060151
<i>Chaenomugil proboscideus</i>	La Paz, Mexico	01 May 2010	F.J. Garcia de Leon	002c	-	-	JQ060658	JQ060409	JQ060152
<i>Chaenomugil proboscideus</i>	La Paz, Mexico	01 May 2010	F.J. Garcia de Leon	002d	-	-	JQ060659	JQ060410	JQ060153
<i>Chelon labrosus</i>	Goulette, Tunisia	22 Dec. 2005	H. Blel	180	-	-	GQ258711	JQ060412	JQ060155
<i>Chelon labrosus</i>	Agadir, Morocco	-	A. Pariselle	178	-	-	JQ060729	JQ060484	JQ060227
<i>Chelon labrosus</i>	Khnefiss, Morocco	Mar. 2010	A. Pariselle	179b	-	-	JQ060660	JQ060411	JQ060154
<i>Chelon macrolepis</i>	Boulouparis, New Caledonia	11 Aug. 2007	P. Borsa	124	-	-	JQ060662	JQ060414	JQ060157
<i>Chelon macrolepis</i>	Koné, New Caledonia	25 Aug. 2007	P. Borsa	132	-	-	JQ060663	JQ060415	JQ060158
<i>Chelon macrolepis</i>	Nouméa, New Caledonia	08 Mar. 2007	P. Borsa	133	MNHN 2009-0803	-	JQ060664	JQ060416	JQ060159
<i>Chelon macrolepis</i>	SW lagoon, New Caledonia	01 Apr. 2007	P. Borsa	135	MNHN 2009-0805	-	JQ060665	JQ060417	JQ060160
<i>Chelon macrolepis</i>	SW lagoon, New Caledonia	01 Apr. 2007	P. Borsa	136	MNHN 2009-0806	-	JQ060666	JQ060418	JQ060161
<i>Chelon macrolepis</i>	Atetsu Bay, Ryukyu Islands, Japan	16 Nov. 2006	K. Shibukawa	137	NMNS-P76044	-	JQ060667	JQ060419	JQ060162
<i>Chelon macrolepis</i>	Taipei, Taiwan	15 June 2008	K.-N. Shen	138	NMMBP10785	-	JQ060668	JQ060420	JQ060163

<i>Chelon macrolepis</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	143	MNHN 2009-0802	-	JQ060669	JQ060421	JQ060164
<i>Chelon macrolepis</i>	Eydhafushi, Baa atoll, Maldives	28 June 2008	P. Borsa, S. Andréfouët	146	-	-	JQ060670	JQ060424	JQ060167
<i>Chelon macrolepis</i>	Mlalazi estuary, South Africa	May 2004	P. Renzo	150	SAIAB-74455	-	JQ060673	JQ060425	JQ060168
<i>Chelon macrolepis</i>	Port Launay, Seychelles	19 Apr. 2005	P.C. Heemstra et al.	151	SAIAB-77876	-	JQ060674	JQ060426	JQ060169
<i>Chelon macrolepis</i>	Ra's al-Hadd, Oman	22 Mar. 2009	P. Bearez	144	MNHN ICOS-00270	-	JQ060671	JQ060422	JQ060165
<i>Chelon macrolepis</i>	Ra's al-Hadd, Oman	22 Mar. 2009	P. Bearez	145	MNHN 2010-0027	-	JQ060672	JQ060423	JQ060166
<i>Chelon macrolepis</i>	Negombo lagoon, Sri Lanka	2007	H. Ashanti	154	-	-	JQ060661	JQ060413	JQ060156
<i>Chelon melinopterus</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	109	(a)	-	JQ060675	JQ060427	JQ060170
<i>Chelon melinopterus</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	111	(a)	-	JQ060676	JQ060428	JQ060171
<i>Chelon planiceps</i>	Kyaiko market, Myanmar	15 Mar. 2008	F. Fang, Thein Win	175	NRM-58400	-	JQ060677	JQ060430	JQ060173
<i>Chelon planiceps</i>	Kyaiko market, Myanmar	15 Mar. 2008	F. Fang, Thein Win	176	NRM-58557	-	JQ060678	JQ060431	JQ060174
<i>Chelon planiceps</i>	Middle part beach, West Alligator Head, NT, Australia	09 June 2001	H. Larson	122	NTM S.15537-001	-	JQ060679	JQ060429	JQ060172
<i>Chelon subviridis</i>	Segara Amahan lagoon, Java, Indonesia	July 2008	S. Kleinertz, SPICE II project	069	-	-	JQ060682	JQ060433	JQ060176
<i>Chelon subviridis</i>	Negombo lagoon, Sri Lanka	2007	H. Ashanti	070	-	-	JQ060681	JQ060434	JQ060177
<i>Chelon subviridis</i>	Cigu, Taiwan	13 Nov. 2008	K.-N. Shen	064	NMMBP10796	-	JQ060680	JQ060432	JQ060175
<i>Crenimugil crenilabis</i>	Moruroa atoll, French Polynesia	June 2006	P. Borsa, M. Kulbicki, G. Mou-Tham	185	MNHN 2009-0808	-	JQ060685	JQ060435	JQ060178
<i>Crenimugil crenilabis</i>	Adhoo atoll, Maldives	28 June 2008	P. Borsa	187	-	-	JQ060683	JQ060436	JQ060179
<i>Crenimugil crenilabis</i>	Moorea, Iles du Vent French Polynesia	24 Mar. 2006	Biocode project	190	MNHN 2008-1002	-	JQ060686	JQ060437	JQ060180
<i>Crenimugil crenilabis</i>	Tahiti, Iles du Vent French Polynesia	Jul.-Aug. 2008	A. Stein	191	-	-	JQ060687	JQ060438	JQ060181
<i>Crenimugil crenilabis</i>	Tuamotu, French Polynesia	Feb. 2009	A. Stein	192	MNHN 2009-1680	-	JQ060688	JQ060439	JQ060182
<i>Crenimugil crenilabis</i>	Saipan, Mariana Islands	24 May 2003	K.A. Moots, E. Heemstra, A.C. Bentley, P.C. Heemstra	193	SAIAB-86172	KU:KUTT:5674	JQ060684	JQ060440	JQ060183
<i>Crenimugil crenilabis</i>	Loop Is., Chesterfield islands, Coral Sea	22 Oct. 2008	P. Borsa	194	-	-	JQ060689	JQ060441	JQ060184
<i>Crenimugil crenilabis</i>	Port Launay (SE beach), Seychelles	19 Apr. 2005	P.C. Heemstra, E. Heemstra, M.J. Smale, A.C. Bentley, et. al.	195	SAIAB-77948	-	JQ060690	JQ060442	JQ060185
<i>Ellochelon vaigiensis</i>	Unspecified location, Australia	31 July 1996	G. Yearsley	046	CSIRO-H4307-01	-	JQ060691	JQ060443	JQ060186
<i>Ellochelon vaigiensis</i>	Batanta Island, West Papua	04 Dec. 2007	P. Borsa	051	-	-	JQ060692	JQ060444	JQ060187
<i>Ellochelon vaigiensis</i>	Tahiti, French Polynesia	01 Aug. 2008	A. Stein	053	-	-	JQ060693	JQ060445	JQ060188
<i>Joturus pichardi</i>	Changuinola River, Boca del Toro, Panama	-	-	022	STRI 21850	-	JQ060694	JQ060446	JQ060189
<i>Liza abu</i>	Tigris River, Turkey	27 Apr. 2005	E. Ünü	061	-	-	JQ060695	JQ060447	JQ060190
<i>Liza affinis</i>	Yunlin, Taiwan	21 Feb. 2008	K.-N. Shen	057x	NMMBP11540	-	JQ060696	JQ060448	JQ060191
<i>Liza alata</i>	Sezela estuary, South Africa	May 2005	A.D. Connell	165	SAIAB-74457	-	JQ060699	JQ060451	JQ060194
<i>Liza alata</i>	East K'monde estuary, South Africa	02 Feb. 2010	P. Cowley	165b	-	-	JQ060700	JQ060452	JQ060195
<i>Liza alata</i>	Charlie's Creek, Daly River NT, Australia	12 June 2007	H. Larson	162	NTM S.16482-001	-	JQ060697	JQ060449	JQ060192
<i>Liza alata</i>	Near Crocodile Creek, Daly River NT, Australia	13 June 2007	H. Larson	164	NTM S.16483-001	-	JQ060698	JQ060450	JQ060193
<i>Liza argentea</i>	unknown location, Australia	25 July 2005	G. Yearsley via Raptis and Sons, Colmslie	037	CSIRO-H4307-04	-	JQ060701	JQ060453	JQ060196
<i>Liza argentea</i>	Port Hacking, NSW, Australia	July 1997	B. Pease et al.	039	AMS I-43204-011	-	JQ060702	JQ060454	JQ060197
<i>Liza argentea</i>	Brisbane, Australia	-	W. Knibb	041	-	-	JQ060703	JQ060455	JQ060198

<i>Liza aurata</i>	Goulette, Tunisia	Apr. 2003	H. Blel	168	-	-	GQ252691	JQ060456	JQ060199
<i>Liza aurata</i>	Agadir, Morocco	-	A. Pariselle	169	-	-	JQ060704	JQ060457	JQ060200
<i>Liza aurata</i>	Dakhla, Western Sahara	Mar. 2010	A. Pariselle	171b	-	-	JQ060705	JQ060458	JQ060201
<i>Liza aurata</i>	Khnfiss, Morocco	Mar. 2010	A. Pariselle	171c	-	-	JQ060706	JQ060459	JQ060202
<i>Liza aurata</i>	Khnfiss, Morocco	Mar. 2010	A. Pariselle	171d	-	-	JQ060707	JQ060460	JQ060203
<i>Liza bandialensis</i>	Saloum estuary, Senegal	2008	O. Diouf	054	MNHN 2009-0790	-	JQ060708	JQ060461	JQ060204
<i>Liza bandialensis</i>	Bubaque, Bijagos Islds, Bissau Guinea	May 2008	Y. Bettarel	056	-	-	JQ060709	JQ060462	JQ060205
<i>Liza dumerili</i>	Toubacouta, Saloum estuary, Senegal	06 Mar. 2009	O. Sadio, J. Raffray	073	SAIAB-83185	-	JQ060710	JQ060463	JQ060206
<i>Liza dumerili</i>	St Louis, Senegal	26 Jan. 2008	J.-D. Durand	076	-	-	JQ060711	JQ060464	JQ060207
<i>Liza dumerili</i>	Fish market, Lome, Togo	19 June 2007	J.-F. Trape	077	-	-	JQ060712	JQ060465	JQ060208
<i>Liza dumerili</i>	Fish market, Bissau, Bissau Guinea	04 May 2010	J.-D. Durand	078b	-	-	JQ060713	JQ060466	JQ060209
<i>Liza dumerili</i>	Great Fish River, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	079	-	-	JQ060714	JQ060467	JQ060210
<i>Liza dumerili</i>	Great Fish River, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	080	-	-	JQ060715	JQ060468	JQ060211
<i>Liza falcipinnis</i>	Toubacouta, Saloum estuary, Senegal	06 Mar. 2009	O. Sadio	083	MNHN 2009-0730	-	JQ060716	JQ060469	JQ060212
<i>Liza falcipinnis</i>	St Louis, Senegal	26 Jan. 2008	J.-D. Durand	084	-	-	JQ060717	JQ060470	JQ060213
<i>Liza falcipinnis</i>	St Louis, Senegal	26 Jan. 2008	J.-D. Durand	085	-	-	JQ060718	JQ060471	JQ060214
<i>Liza falcipinnis</i>	Fish market, Lome, Togo	19 June 2007	J.-F. Trape	086	-	-	JQ060719	JQ060472	JQ060215
<i>Liza grandisquamis</i>	Saloum, Sénégal	06 Mar. 2009	O. Sadio, J. Raffray, L. Tito	088	-	-	JQ060720	JQ060473	JQ060216
<i>Liza grandisquamis</i>	Fish market, Bissau, Bissau Guinea	04 May 2010	J.-D. Durand	089b	-	-	JQ060721	JQ060474	JQ060217
<i>Liza grandisquamis</i>	Saloum, Sénégal	06 Mar. 2009	O. Sadio	090	MNHN 2009-731	-	JQ060722	JQ060475	JQ060218
<i>Liza grandisquamis</i>	Saloum, Sénégal	06 Mar. 2009	O. Sadio	091	SAIAB-83182	-	JQ060723	JQ060476	JQ060219
<i>Liza haematocheila</i>	Yunlin, Taiwan	03 Dec. 2007	K.-N. Shen	095	-	-	JQ060724	JQ060477	JQ060220
<i>Liza haematocheila</i>	Yunlin, Taiwan	03 Dec. 2007	K.-N. Shen	102	NMMBP11541	-	JQ060725	JQ060478	JQ060221
<i>Liza ramada</i>	Goulette, Tunisia	Apr. 2003	H. Blel	173	-	-	GQ258707	JQ060479	JQ060222
<i>Liza ramada</i>	Zerga, Morocco	Mar. 2010	A. Pariselle	174b	-	-	JQ060726	JQ060480	JQ060223
<i>Liza richardsonii</i>	Orange River, Namibia	12 June 2001	J. Koekemoer	157	SAIAB-64270	-	JQ060727	JQ060481	JQ060224
<i>Liza richardsonii</i>	Great Fish River, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	158	-	-	JQ060728	JQ060482	JQ060225
<i>Liza saliens</i>	Goulette, Tunisia	Apr. 2003	H. Blel	166	-	-	GQ258709	JQ060483	JQ060226
<i>Liza</i> sp.	Saint Lucia, South Africa	14 May 2005	A.K. Whitfield, J.-D. Durand, J. Panfili	161	SAIAB-78131	-	JQ060734	JQ060492	JQ060235
<i>Liza</i> sp.	Al Khobar, Saudia Arabia, Persian Gulf	Nov.-Dec. 2008	Z. Batang, P. Premlal	113	-	-	JQ060736	JQ060490	JQ060233
<i>Liza</i> sp.	Al Khobar, Saudia Arabia, Persian Gulf	Nov.-Dec. 2008	Z. Batang, P. Premlal	114	-	-	JQ060737	JQ060491	JQ060234
<i>Liza</i> sp.	Pangasinan, Philippines	01 July 2008	B. W. Jamandre	103	-	-	JQ060730	JQ060487	JQ060230
<i>Liza</i> sp.	Pangasinan, Philippines	01 July 2008	B. W. Jamandre	107	-	-	JQ060731	JQ060488	JQ060231
<i>Liza</i> sp.	Negombo lagoon, Sri Lanka	2007	H. Ashanti	062	-	-	JQ060732	JQ060485	JQ060228
<i>Liza</i> sp.	Ho Chi Minh City, Viet Nam	20 Mar. 2010	W.-J. Chen	062b	NMMBP11557	-	JQ060739	JQ060493	JQ060237
<i>Liza</i> sp.	Cigu, Taiwan	13 Nov. 2008	K.-N. Shen	063	NMMBP10791	-	JQ060733	JQ060486	JQ060229
<i>Liza</i> sp.	Quang Yen, Viet Nam	21 Mar. 2010	W.-J. Chen	057b	NMMBP11558	-	JQ060738	JQ060494	JQ060236
<i>Liza</i> sp.	Yilan, Taiwan	22 July 2002	L.-C. Chaung	108	NMMBP10802	-	JQ060735	JQ060489	JQ060232
<i>Liza tricuspidens</i>	Sunday estuary, South Africa	08 Aug. 2007	A.K. Whitfield	155	-	-	JQ060740	JQ060495	JQ060238
<i>Moolgarda cunnesius</i>	Great Fish River, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	278	-	-	JQ060741	JQ060498	JQ060241

<i>Moolgarda cunnesius</i>	Beach 1Km S of McGowans Beach, Kalumburu, Australia	06 Sep. 1992	J. Paxton	275	AMS-I-33460-016	-	JQ060743	JQ060496	JQ060239
<i>Moolgarda cunnesius</i>	Don Son Town, Vietnam	22 Mar. 2010	W.-J. Chen	276b	NMMBP11559	-	JQ060744	JQ060499	JQ060242
<i>Moolgarda cunnesius</i>	Yunlin, Taiwan	05 May 2002	K.-T. Shao	276	ASIZP0061397	-	JQ060742	JQ060497	JQ060240
<i>Moolgarda engeli</i>	Saipan, Mariana Islands	24 May 2003	K.A. Moots, E. Heemstra, A.C. Bentley, P.C. Heemstra	198	KU:KUI:32523	KU:KUIT:5667	JQ060745	JQ060500	JQ060243
<i>Moolgarda engeli</i>	Hawaii	June-Oct. 2008	T.K. Ogawa	200	-	-	JQ060746	JQ060501	JQ060244
<i>Moolgarda engeli</i>	Moorea, Iles du Vent, French Polynesia	15 Mar. 2006	S. Planes, Campagne Biocode	201	MNHN 2008-0692	-	JQ060747	JQ060502	JQ060245
<i>Moolgarda engeli</i>	Tahiti, Iles du Vent, French Polynesia	01 Aug. 2008	A. Stein	203	-	-	JQ060748	JQ060503	JQ060246
<i>Moolgarda perusii</i>	Foué, New Caledonia	18 Aug. 2007	P. Borsa	264	MNHN 2009-0811	-	JQ060749	JQ060504	JQ060247
<i>Moolgarda perusii</i>	Taisi, Taiwan	15 June 2008	K.-N. Shen	274	NMMBP10798	-	JQ060750	JQ060505	JQ060248
<i>Moolgarda sebeli</i>	Eydhafushi, Baa Atoll, Maldives	28 June 2008	P. Borsa, S. Andréfouët	209	-	-	JQ060888	JQ060631	JQ060382
<i>Moolgarda sebeli</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	213	-	-	JQ060889	JQ060632	JQ060383
<i>Moolgarda sebeli</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	214	-	-	JQ060890	JQ060633	JQ060384
<i>Moolgarda sebeli</i>	SW Lagoon, New Caledonia	08 Apr. 2007	P. Borsa	204	-	-	JQ060751	JQ060506	JQ060249
<i>Moolgarda sebeli</i>	Aurora Province, Philippines	01 July 2008	B.W. Jamandre	205	-	-	JQ060752	JQ060507	JQ060250
<i>Moolgarda sebeli</i>	Taisi, Taiwan	15 June 2008	K.-N. Shen	206	NMMBP10777	-	JQ060753	JQ060508	JQ060251
<i>Moolgarda sebeli</i>	Batanta Island, West Papua	04 Dec. 2007	P. Borsa	207	-	-	JQ060754	JQ060509	JQ060252
<i>Moolgarda sebeli</i>	Garapan Lagoon off Oceanside Bar, Saipan, Mariana Island	24 May 2003	K.A. Moots, E. Heemstra, A.C. Bentley, P.C. Heemstra	210	-	KU:KUIT:5647	JQ060755	JQ060510	JQ060253
<i>Moolgarda sebeli</i>	Al Khobar, Saudi Arabia, Persian Gulf	Nov.-Dec. 2008	Z. Batang, P. Premlal	217	-	-	JQ060756	JQ060511	JQ060254
<i>Moolgarda sebeli</i>	Ternay Bay, Seychelles	14 May 2005	P.C. Heemstra, E. Heemstra, M.J. Smale, A.C. Bentley, <i>et. al.</i>	220	SAIAB-77896	-	JQ060758	JQ060513	JQ060256
<i>Moolgarda sebeli</i>	Stone Town, Zanzibar, Tanzania	28 May 2010	J.-D. Durand	221a	-	-	JQ060891	JQ060634	JQ060385
<i>Moolgarda sebeli</i>	Noumea, New Caledonia	08 Mar. 2007	P. Borsa	225	MNHN 2009-0815	-	JQ060759	JQ060514	JQ060257
<i>Moolgarda sebeli</i>	Noumea, New Caledonia	25 Aug. 2007	P. Borsa	226	MNHN 2009-0810	-	JQ060760	JQ060515	JQ060258
<i>Moolgarda sebeli</i>	Mackay harbour boat ramp, Queensland, Australia	25 June 1997	CRIMP	232	CSIRO-H4596-01	-	JQ060761	EF609494	JQ060259
<i>Moolgarda sebeli</i>	South Goulburn Island, NT, Australia	30 Nov. 2004	R. Williams	234	NTM S.16014-002	-	JQ060762	JQ060516	JQ060260
<i>Moolgarda sebeli</i>	Fish River, Daly River area, NT, Australia	06 Sep. 2001	R. Williams	235	NTM S.15362-001	-	JQ060763	JQ060517	JQ060261
<i>Moolgarda sebeli</i>	Port Launay (SE beach), Seychelles	19 May 2005	P.C. Heemstra, E. Heemstra, M.J. Smale, A.C. Bentley, <i>et. al.</i>	218	SAIAB-77947	-	JQ060757	JQ060512	JQ060255
<i>Moolgarda sp.</i>	La Réunion	Oct. 2008	P. Durville, N. Hubert	212	MNHN 2011-0097	-	JQ060765	JQ060518	JQ060262
<i>Moolgarda sp.</i>	Ra's al-Hadd, Oman	21 Mar. 2009	P. Bearez	215	MNHN ICOS-00266	-	JQ060768	JQ060522	JQ060266
<i>Moolgarda sp.</i>	Negombo lagoon, Sri Lanka	2007	H. Ashanti	221	-	-	JQ060766	JQ060519	JQ060263
<i>Moolgarda sp.</i>	La Réunion	Oct. 2008	P. Durville, N. Hubert	222	MNHN 2011-0096	-	JQ060767	JQ060520	JQ060264
<i>Mugil bananensis</i>	Saloum estuary, Senegal	06 Mar. 2009	O. Sadio, J. Raffray, L. Tito	286	MNHN 2009-0733	-	JQ060769	JQ060523	JQ060267
<i>Mugil bananensis</i>	Ebrie lagoon, Ivory Coast	Aug. 2007	B. Gourene	289	-	-	JQ060770	JQ060524	JQ060268
<i>Mugil capurrii</i>	St Louis, Senegal estuary, Sénégal	26 Jan. 2008	J.-D. Durand	282	-	-	HM143894	JQ060525	JQ060269
<i>Mugil capurrii</i>	Dakhla, Western Sahara	June 2006	H. Masski	283	-	-	HM143895	JQ060526	JQ060270

<i>Mugil capurrii</i>	Lomé, Togo	19 June 2007	J.-F. Trape	285	MNHN 2009-0795	-	HM143896	JQ060527	JQ060271
<i>Mugil cephalus</i>	Martigues, France	02 Aug. 2007	G. Lepra	321	-	-	JQ060817	JQ060533	JQ060277
<i>Mugil cephalus</i>	Goulette, Tunisia	22 Dec. 2005	H. Blel	319	-	-	JQ060816	JQ060532	JQ060276
<i>Mugil cephalus</i>	Merja Zerga, Morocco	09 Feb. 2006	H. Nouiri	314	-	-	JQ060815	JQ060529	JQ060273
<i>Mugil cephalus</i>	Agadir, Morocco	-	A. Pariselle	322	-	-	JQ060818	JQ060534	JQ060278
<i>Mugil cephalus</i>	Khniass, Morocco	Mar. 2010	A. Pariselle	325c	-	-	JQ060819	JQ060536	JQ060280
<i>Mugil cephalus</i>	Coast of Iquique, Chili	23 May 2005	M. Nirchio	375	UDOV-290	-	JQ060790	JQ060563	JQ060311
<i>Mugil cephalus</i>	Coast of Iquique, Chili	23 May 2005	M. Nirchio	376	UDOV-291	-	JQ060791	JQ060564	JQ060312
<i>Mugil cephalus</i>	Charleston, South Carolina, USA	09 May 2005	B. Roumillat	347	-	-	JQ060787	HQ149710	JQ060294
<i>Mugil cephalus</i>	Indian River, Florida, USA	01 June 2005	R. Paperno	344	-	-	JQ060786	HQ149711	JQ060293
<i>Mugil cephalus</i>	Laguna madre, Mexico	June 2006	F. J. Garcias de Leon	373	-	-	JQ060788	JQ060562	JQ060310
<i>Mugil cephalus</i>	Kaoping estuary, Taiwan	28 Dec. 2007	K.-N. Shen	329	NMMBP11545	-	JQ060789	JQ060540	JQ060284
<i>Mugil cephalus</i>	Hawaii	June-Oct. 2008	T. Ogawa	350	-	-	JQ060820	JQ060549	JQ060296
<i>Mugil cephalus</i>	Hawaii	June-Oct. 2008	T. Ogawa	351	-	-	JQ060821	JQ060550	JQ060297
<i>Mugil cephalus</i>	Hawaii	Oct. 2008	M.T. Craig	354b	-	-	JQ060822	JQ060551	JQ060298
<i>Mugil cephalus</i>	Great Fish river estuary, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	341	-	-	JQ060807	JQ060544	JQ060288
<i>Mugil cephalus</i>	Great Fish river estuary, South Africa	12 May 2005	A.K. Whitfield, J.-D. Durand	342	-	-	JQ060810	JQ060545	JQ060289
<i>Mugil cephalus</i>	St Lucia, South Africa	May, Nov. 2006	A.K. Whitfield	343	-	-	JQ060808	JQ060546	JQ060290
<i>Mugil cephalus</i>	St Lucia, South Africa	May, Nov. 2006	A.K. Whitfield	343b	-	-	JQ060809	JQ060547	JQ060291
<i>Mugil cephalus</i>	St Lucia, South Africa	May, Nov. 2006	A.K. Whitfield	343c	-	-	JQ060811	JQ060548	JQ060292
<i>Mugil cephalus</i>	SW Lagoon, New Caledonia	25 Aug. 2007	P. Borsa	388	-	-	JQ060805	JQ060572	JQ060321
<i>Mugil cephalus</i>	Pateu Dam, New Zeland	03 Nov. 2006	J. Boubee	361	-	-	JQ060804	JQ060554	JQ060301
<i>Mugil cephalus</i>	Pateu Dam, New Zeland	03 Nov. 2006	J. Boubee	362	-	-	JQ060806	JQ060555	JQ060302
<i>Mugil cephalus</i>	La Paz, Mexico	23 June 2006	F.J. Garcia de Leon	371	-	-	JQ060775	HQ149715	JQ060307
<i>Mugil cephalus</i>	Paredon, Chiapas, Mexico	Apr. 2010	P. Diaz Jaimes	371b	-	-	JQ060776	JQ060560	JQ060308
<i>Mugil cephalus</i>	Paredon, Chiapas, Mexico	Apr. 2010	P. Diaz Jaimes	371c	-	-	JQ060777	JQ060561	JQ060309
<i>Mugil cephalus</i>	Lima, Peru	21-24 June 2005	S. Sirvas	349	-	-	JQ060774	HQ149714	JQ060295
<i>Mugil cephalus</i>	Waikato river, New Zeland	28 June 1905	J. Boubee	362b	-	-	JQ060812	JQ060556	JQ060303
<i>Mugil cephalus</i>	Swansea, Sydney, Australia	17 Nov. 2005	K. Rowling	367	-	-	JQ060813	JQ060558	JQ060305
<i>Mugil cephalus</i>	Port Hacking, Point Danger, Sydney, Australia	July 1997	B. Pease <i>et al.</i>	377	AMS-I-43204-082	-	JQ060814	JQ060565	JQ060313
<i>Mugil cephalus</i>	Kaoping estuary, Taiwan	29 Dec. 2007	K.-N. Shen	328	NMMBP11549	-	JQ060801	JQ060539	JQ060283
<i>Mugil cephalus</i>	Taipei, Taiwan	15 June 2008	K.-N. Shen	357	NMMBP10790	-	JQ060802	JQ060552	JQ060299
<i>Mugil cephalus</i>	Pearl River, China	May 2005	X.-P. Nie	358	-	-	JQ060803	JQ060553	JQ060300
<i>Mugil cephalus</i>	Atake river, Kagoshima Prefecture, Kyushu, Japan	04 July 2007	S. Chiba	365	NSMT-P77767	-	JQ060800	JQ060557	JQ060304
<i>Mugil cephalus</i>	Khniass, Morocco	Mar. 2010	A. Pariselle	325b	-	-	JQ060795	JQ060535	JQ060279
<i>Mugil cephalus</i>	Saloum estuary, Senegal	Dec. 2005	K. Diop	308	-	-	JQ060792	JQ060528	JQ060272
<i>Mugil cephalus</i>	Hann Bay, Dakar, Senegal	06 Mar. 2009	J.-D. Durand	326	MNHN 2009-734	-	JQ060796	JQ060537	JQ060281

<i>Mugil cephalus</i>	Hann Bay, Dakar, Senegal	06 Mar. 2009	J.-D. Durand	327	SAIAB-83187	-	JQ060797	JQ060538	JQ060282
<i>Mugil cephalus</i>	Boran Dabon, Forecariah estuary, Guinea	20 Feb. 2006	S.B. Camara	337	-	-	JQ060798	JQ060543	JQ060287
<i>Mugil cephalus</i>	Lomé, Togo	19 June 2007	J.-F. Trape	333	-	-	JQ060799	JQ060542	JQ060286
<i>Mugil cephalus</i>	Nokoue Lake, Benin	12 Apr. 2007	P. Laleye	315	-	-	JQ060793	JQ060530	JQ060274
<i>Mugil cephalus</i>	Cunene River, Angola	-	S. Lamberth	316	-	-	JQ060794	JQ060531	JQ060275
<i>Mugil cephalus</i>	Peel Harvey estuary, Australia	05 Jan. 2006	K. Smith	368	-	-	JQ060785	JQ060559	JQ060306
<i>Mugil cephalus</i>	Kaoping estuary, Taiwan	29 Dec. 2007	K.-N. Shen	329b	NMMBP11553	-	JQ060778	JQ060541	JQ060285
<i>Mugil cephalus</i>	Koné, New Caledonia	11 Aug. 2007	P. Borsa	380	MNHN 2009-0819	-	JQ060779	JQ060566	JQ060314
<i>Mugil cephalus</i>	Noumea, New Caledonia	08 Apr. 2007	P. Borsa	383	MNHN 2009-0820	-	JQ072903	JQ060568	JQ060316
<i>Mugil cephalus</i>	Koné, New Caledonia	11 Aug. 2007	P. Borsa	384	-	-	JQ060781	JQ060569	JQ060317
<i>Mugil cephalus</i>	Koné, New Caledonia	11 Aug. 2007	P. Borsa	385	-	-	JQ060782	JQ072904	JQ060318
<i>Mugil cephalus</i>	Koné, New Caledonia	11 Aug. 2007	P. Borsa	386	-	-	JQ060783	JQ060570	JQ060319
<i>Mugil cephalus</i>	Koné, New Caledonia	11 Aug. 2007	P. Borsa	387	-	-	JQ060784	JQ060571	JQ060320
<i>Mugil cephalus</i>	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	381	-	-	JQ060780	JQ060567	JQ060315
<i>Mugil curema</i>	Arroyo Zanja, Uruguay	21 Feb. 2007	S. Kullander	417	NRM-56494	-	JQ060854	JQ060605	JQ060354
<i>Mugil curema</i>	Arroyo Zanja, Uruguay	21 Feb. 2007	S. Kullander	418	NRM-56495	-	JQ060855	JQ060606	JQ060355
<i>Mugil curema</i>	Upper Cooper River, USA	14 Oct. 2005	B. Roumillat	404	-	-	JQ060827	JQ060586	JQ060335
<i>Mugil curema</i>	Close to Michaels Rock , Guanaja Island, Honduras	15 July 2008	W.A. Matamoros	405	USMI field no. WAM08-118	-	JQ060823	JQ060587	JQ060336
<i>Mugil curema</i>	Laguna Madre, Mexico	July 2006	F.J. Garcia de Leon	407	-	-	JQ060829	JQ060589	JQ060338
<i>Mugil curema</i>	Itapissuma, Brazil	03 Dec. 2004	R. Lessa	408	-	-	JQ060828	JQ060590	JQ060339
<i>Mugil curema</i>	Guadeloupe	30 June 1905	M. Louis	411	-	-	JQ060825	JQ060591	JQ060340
<i>Mugil curema</i>	La Restinga, Margarita Island, Venezuela	25 Jan. 2005	M. Nirchio	414	UDOV-201 (b)	-	JQ060824	JQ060593	JQ060342
<i>Mugil curema</i>	Saloum estuary, Senegal	06 Mar. 2009	O. Sadio	390	MNHN 2009-0732	-	JQ060843	JQ060575	JQ060324
<i>Mugil curema</i>	Nokoue, Lake, Benin	12 Apr. 2007	P. Laleye	393	-	-	JQ060846	JQ060578	JQ060327
<i>Mugil curema</i>	Nokoue, Lake, Benin	12 Apr. 2007	P. Laleye	394	-	-	JQ060849	JQ060579	JQ060328
<i>Mugil curema</i>	Lomé, Togo	19 June 2007	J.-F. Trape	396	-	-	JQ060847	JQ060580	JQ060329
<i>Mugil curema</i>	Lomé, Togo	19 June 2007	J.-F. Trape	397	-	-	JQ060848	JQ060581	JQ060330
<i>Mugil curema</i>	Saloum estuary, Senegal	06 Mar. 2009	O. Sadio	391	SAIAB-83183	-	JQ060844	JQ060576	JQ060325
<i>Mugil curema</i>	Foundiougne, Saloum estuary, Senegal	Dec. 2005	O. Diouf	392	-	-	JQ060845	JQ060577	JQ060326
<i>Mugil curema</i>	La Restinga, Margarita Island, Venezuela	06 Apr. 2004	M. Nirchio	399	UDOV-69 (c)	-	JQ060842	JQ060582	JQ060331
<i>Mugil curema</i>	La Restinga, Margarita Island, Venezuela	06 Apr. 2004	M. Nirchio	400	UDOV-70 (c)	-	JQ060839	JQ060583	JQ060332
<i>Mugil curema</i>	Boca del Río, Margarita Island, Venezuela	12 Apr. 2004	M. Nirchio	401	UDOV-73 (c)	-	JQ060840	JQ060584	JQ060333
<i>Mugil curema</i>	Boca del Río, Margarita Island, Venezuela	10 Apr. 2004	M. Nirchio	403	UDOV-71 (c)	-	JQ060841	JQ060585	JQ060334
<i>Mugil curema</i>	La Paz, Mexico	23 June 2006	F.J. Garcia de Leon	406	-	-	JQ060830	JQ060588	JQ060337
<i>Mugil curema</i>	Barra San José, Chapas, Mexico	Apr. 2010	N. Laurrabaquio Alvarado	422	-	-	JQ060834	JQ060596	JQ060345
<i>Mugil curema</i>	Barra de Santiago, El Salvador	25 Feb. 2006	S. Kullander	415	NRM-53693	-	JQ060856	JQ060604	JQ060353
<i>Mugil curema</i>	Paredon, Chapas, Mexico	09 Apr. 2010	N. Laurrabaquio Alvarado	425	-	-	JQ060837	JQ060599	JQ060348
<i>Mugil curema</i>	Mouth of Cerique estuary, El Salvador	20 June 2008	A.C. Bentley, K. Lara	432	KU:KUI:40336	KU:KUIT:8547	JQ060852	JQ060603	JQ060352
<i>Mugil curema</i>	Chorreras Bay, Panama, Pacific coast	05 Dec. 1999	M. Nirchio	293	UDOV-186 (d)	-	JQ060832	JQ060573	JQ060322
<i>Mugil curema</i>	Chorreras Bay, Panama, Pacific coast	05 Dec. 1999	M. Nirchio	294	UDOV-187 (d)	-	JQ060833	JQ060574	JQ060323
<i>Mugil curema</i>	Barra San José, Chapas, Mexico	08 Apr. 2010	N. Laurrabaquio Alvarado	423	-	-	JQ060835	JQ060597	JQ060346

<i>Mugil curema</i>	Barra San José, Chapas, Mexico	08 Apr. 2010	N. Laurrabaquio Alvarado	424	-	-	JQ060836	JQ060598	JQ060347
<i>Mugil curema</i>	North Peru	2005	S. Sirvas	413	-	-	JQ060831	JQ060592	JQ060341
<i>Mugil curema</i>	Salango, Ecuador	11 Nov. 2008	P. Béarez	420	-	-	JQ060838	JQ060595	JQ060344
<i>Mugil curema</i>	Sand flats at mouth of Cerique Estuary, El Salvador	16 June 2008	A.C. Bentley, K. Lara	426	KU:KUI:40290	KU:KUTT:8483	JQ060850	JQ060600	JQ060349
<i>Mugil curema</i>	St. Johns college shore, Belize City, Belize	08 July 1999	Belize Workshop participants	419	-	KU:KUTT:5847	JQ060826	JQ060594	JQ060343
<i>Mugil curema</i>	Sand flats at mouth of Cerique Estuary, El Salvador	16 June 2008	A.C. Bentley, K. Lara	429	KU:KUI:40290	KU:KUTT:8510	JQ060851	JQ060601	JQ060350
<i>Mugil curema</i>	Mangrove upstream Cerique estuary, El Salvador	16 June 2008	A.C. Bentley, K. Lara	430	-	KU:KUTT:8527	JQ060853	JQ060602	JQ060351
<i>Mugil hospes</i>	West side of Turneffe Caye, deep hole, Belize	08 July 1999	Belize Workshop participants	306	-	KU:KUTT:5833	JQ060857	JQ060607	JQ060356
<i>Mugil incilis</i>	Kourou, French Guyana	12 Jan. 2007	R. Vigouroux	302	-	-	JQ060858	JQ060608	JQ060357
<i>Mugil incilis</i>	Kourou, French Guyana	12 Jan. 2007	R. Vigouroux	299	-	-	JQ060859	JQ060609	JQ060358
<i>Mugil liza</i>	Arroyo Zanja, Uruguay	21 Feb. 2007	S. Kullander	378	NRM-56496	-	JQ060862	JQ060610	JQ060361
<i>Mugil liza</i>	Kourou, French Guyana	13 Jan. 2007	R. Vigouroux	295	-	-	JQ060860	HQ149712	JQ060359
<i>Mugil liza</i>	La Restiga, Margarita Island, Venezuela	26 June 2004	M. Nirchio	298	UDOV-89	-	JQ060861	HQ149713	JQ060360
<i>Mugil liza</i>	Laguna del Diaro, Uruguay	21 Feb. 2007	S. Kullander	379	NRM-55970	-	JQ060863	JQ060611	JQ060362
<i>Mugil rubrioculus</i>	Boca del Rio, Margarita Island, Venezuela	01 June 2004	M. Nirchio	305	UDOV-88	-	JQ060864	JQ060612	JQ060363
<i>Mugil rubrioculus</i>	Chorreras Bay, Pacific coast of Panama	05 Dec. 1999	M. Nirchio	305b	UDOV-190	-	JQ060865	JQ060613	JQ060364
<i>Mugil trichodon</i>	Boca del Rio, Margarita Island, Venezuela	10 Apr. 2004	M. Nirchio	291	UDOV-72	-	JQ060866	JQ060614	JQ060365
<i>Myxus capensis</i>	East Kleinemonde estuary, South Africa	21 Sep. 2007	A.K. Whitfield	019	-	-	JQ060867	JQ060615	JQ060366
<i>Myxus elongatus</i>	unknown location, Australia	29 July 2003	Sydney Wholesale Fish Market	020	NMV A 25183-002	-	JQ060868	JQ060616	JQ060367
<i>Neomyxus leuciscus</i>	Saipan, Mariana Islands	24 May 2003	K.A. Moots, E. Heemstra, A.C. Bentley, P.C. Heemstra	003	SAIAB-86170	KUI:KUTT:5673	JQ060869	JQ060617	JQ060368
<i>Neomyxus leuciscus</i>	Arutua atoll, Tuamotu	Nov. 2009	A. Stein	003b	MNHN 2009-1681	-	JQ060870	JQ060618	JQ060369
<i>Oedalechilus labeo</i>	Goulette, Tunisia	Apr. 2003	H. Blel	181	-	-	JQ060871	JQ060619	JQ060370
<i>Oedalechilus labiosus</i>	Orchid Island, Taiwan	01 Jan. 2009	K.-N. Shen	243	NMMBP10775	-	JQ060872	JQ060620	JQ060371
<i>Paramugil parmatius</i>	Segara Amahan lagoon, Java, Indonesia	July 2008	S. Kleinertz, SPICE II project	118	-	-	JQ060873	JQ060621	JQ060372
<i>Rhinomugil corsula</i>	Mandalay fish market, Myanmar	26 Mar. 2008	S. Kullander, T.-Y. Liao	016	NRM 59032	-	JQ060874	JQ060622	JQ060373
<i>Rhinomugil nasutus</i>	Near Crocodile Creek, Daly river, NT, Australia	13 June 2007	H. Larson	015	NTM S.16483-002	-	JQ060875	JQ060623	JQ060374
<i>Sicamugil cascasia</i>	Dhaka, Bangladesh	13 Dec. 2008	R.L. Mayden <i>et al.</i>	013	FNHM 172496	-	JQ060876	JQ060624	JQ060375
<i>Sicamugil hamiltonii</i>	Myoma market, Myanmar	18 Mar. 2008	F. Fang, Thein Win	014	NRM 58582	-	JQ060877	JQ060625	JQ060376
<i>Trachystoma petardi</i>	Williams River, Queensland, Australia	16 Feb. 2004	M. Charlton	017	AMS I-43255-002	-	JQ060878	JQ060626	JQ060377
<i>Valamugil buchanani</i>	New Caledonia	08 Apr. 2007	P. Borsa	245	MNHN 2009-0816	-	JQ060879	JQ060627	JQ060378
<i>Valamugil buchanani</i>	Umgazana, South Africa	12 May 2006	DIFS	254	SAIAB-78293	-	JQ060880	JQ060628	JQ060379
<i>Valamugil buchanani</i>	Kenya	Jul.-Nov. 2008	D. Nyngi	248	-	-	JQ060894	JQ060641	JQ060392
<i>Valamugil buchanani</i>	Kenya	Jul.-Nov. 2008	D. Nyngi	252	-	-	JQ060893	JQ060642	JQ060393
<i>Valamugil robustus</i>	Nkadusweni estuary, South Africa	09 May 2006	DIFS	259	SAIAB-78094	-	JQ060881	JQ060629	JQ060380
<i>Valamugil robustus</i>	Poenskop, South Africa	10 May 2006	DIFS	260	SAIAB-78137	-	JQ060882	JQ060630	JQ060381
<i>Valamugil robustus</i>	Réunion Island	Oct. 2008	P. Durville, N. Hubert	255	MNHN 2011-0095	-	JQ060764	JQ060521	JQ060265
<i>Valamugil</i> sp.	Aurora Province, Philippines	01 July 2008	B.W. Jamandre	268	-	-	JQ060883	JQ060639	JQ060390

<i>Valamugil</i> sp.	Negombo lagoon, Sri Lanka	2007	H. Ashanti	271	-	-	JQ060884	JQ060640	JQ060391
<i>Valamugil</i> sp.	Nha Trang City, Khanh Hoa Province, Viet Nam	25 Feb. 2009	D. Vo	229	-	-	JQ060892	JQ060635	JQ060386
<i>Valamugil</i> sp.	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	238	(c)	-	JQ060885	JQ060636	JQ060387
<i>Valamugil</i> sp.	Viti Levu, Fiji	19 Sep. 2008	P. Borsa	239	(c)	-	JQ060886	JQ060637	JQ060388
<i>Valamugil</i> sp.	Pingdon, Taiwan	15 Aug. 2004	P.-F. Lee	241	ASIZP0064762	-	JQ060887	JQ060638	JQ060389

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
- (c) karyotype: 2n = 24 chromosomes
- (b) 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

Primers used for the PCR amplification and sequencing of mitochondrial *16S*rRNA, *COI*, and *cytb* gene fragments in Mugilidae.

T: annealing temperature

Gene, Primer name	Sequence	<i>T</i>	Reference
<i>16S</i>			
<i>16S</i> ARL	5'-CGCCTGTTTATCAAAAACAT-3'	50°C	Palumbi et al. (1991)
<i>16S</i> BRH	5'-CCGGTCTGAACTCAGATCACGT-3'	50°C	Palumbi et al. (1991)
<i>16S</i> 145-F	5'-GTACCGCAAGGGAACGCTGA-3'	50°C	present study
<i>16S</i> 1100-R	5'-TAGGGTCTTCTCGTCTTATG-3'	50°C	present study
<i>COI</i>			
<i>FishF1</i>	5'-TCAACCAACCACAAAGACATTGGCAC-3'	52°C	Ward et al. (2005)
<i>COI</i> 649-F	5'-ACATCCTTCTTYGACCCWGC-3'	52°C	present study
<i>FishR1</i>	5'-TAGACTTCTGGGTGGCCAAAGAATCA-3'	52°C	Ward et al. (2005)
<i>FishR2</i>	5'-ACTTCAGGGTGACCGAAGAATCAGAA-3'	52°C	Ward et al. (2005)
<i>FishR4</i>	5'-CTGTGAACATGTGATGGGCTC-3'	52°C	present study
<i>Fish-R5</i>	5'-ACGTAGTGGAAATGGGCTAC-3'	52°C	present study
<i>FishSer-R5</i>	5'-GTTCTGACTCCTCCCTTTCTCG-3'	52°C	present study
<i>cytb</i>			
<i>FishcytB-F</i>	5'-ACCACCGTTGTTATTCAACTACAAGAAC-3'	52°C	Sevilla et al. (2007)
<i>GluMug 1F</i>	5'-GGCTTGAAAAACCACCGTTG-3'	52°C	present study
<i>Cytob610-F</i>	5'-GAAACAGGCTCAAAAYAYCC-3'	52°C	present study
<i>MixCytob937-2R</i>	5'-GGKCGGAATGTYAGGCTTCG-3'	52°C	present study
<i>TrucytB-R</i>	5'-CCGACTTCCGGATTACAAGACCG-3'	52°C	Sevilla et al. (2007)

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)

Genus	Δ	P
<i>Sicamugil</i>	0.3	0.985
<i>Agonostomus</i>	4.6	0.944
<i>Rhinomugil</i>	108.5	0.008
<i>Valamugil</i>	145.5	< 0.001
<i>Myxus</i>	191.0	< 0.0001
<i>Oedalechilus</i>	252.9	< 0.0001
<i>Liza</i>	284.7	< 0.0001
<i>Moolgarda</i>	550.4	< 0.0001

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.

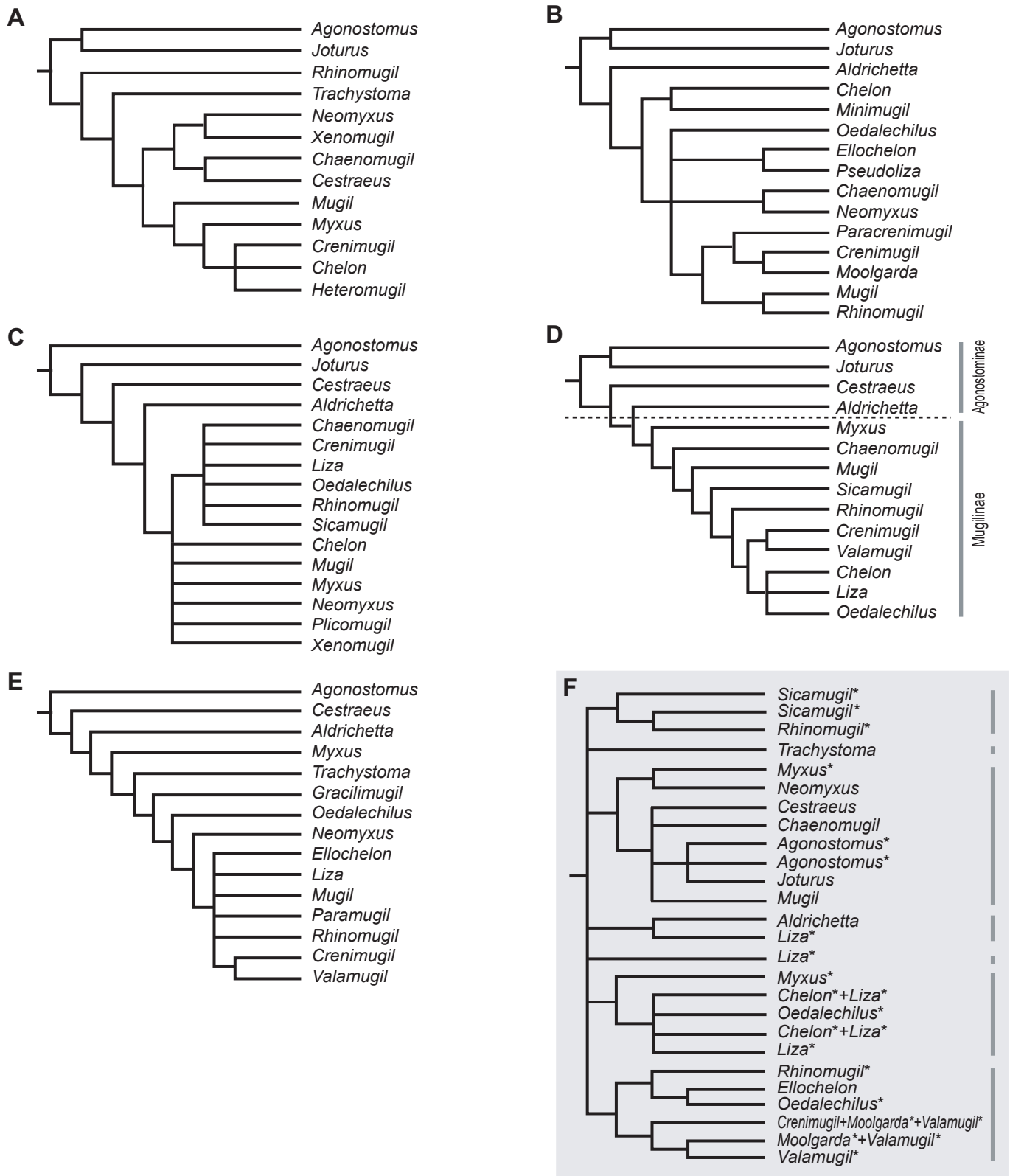


Fig 1 Durand et al

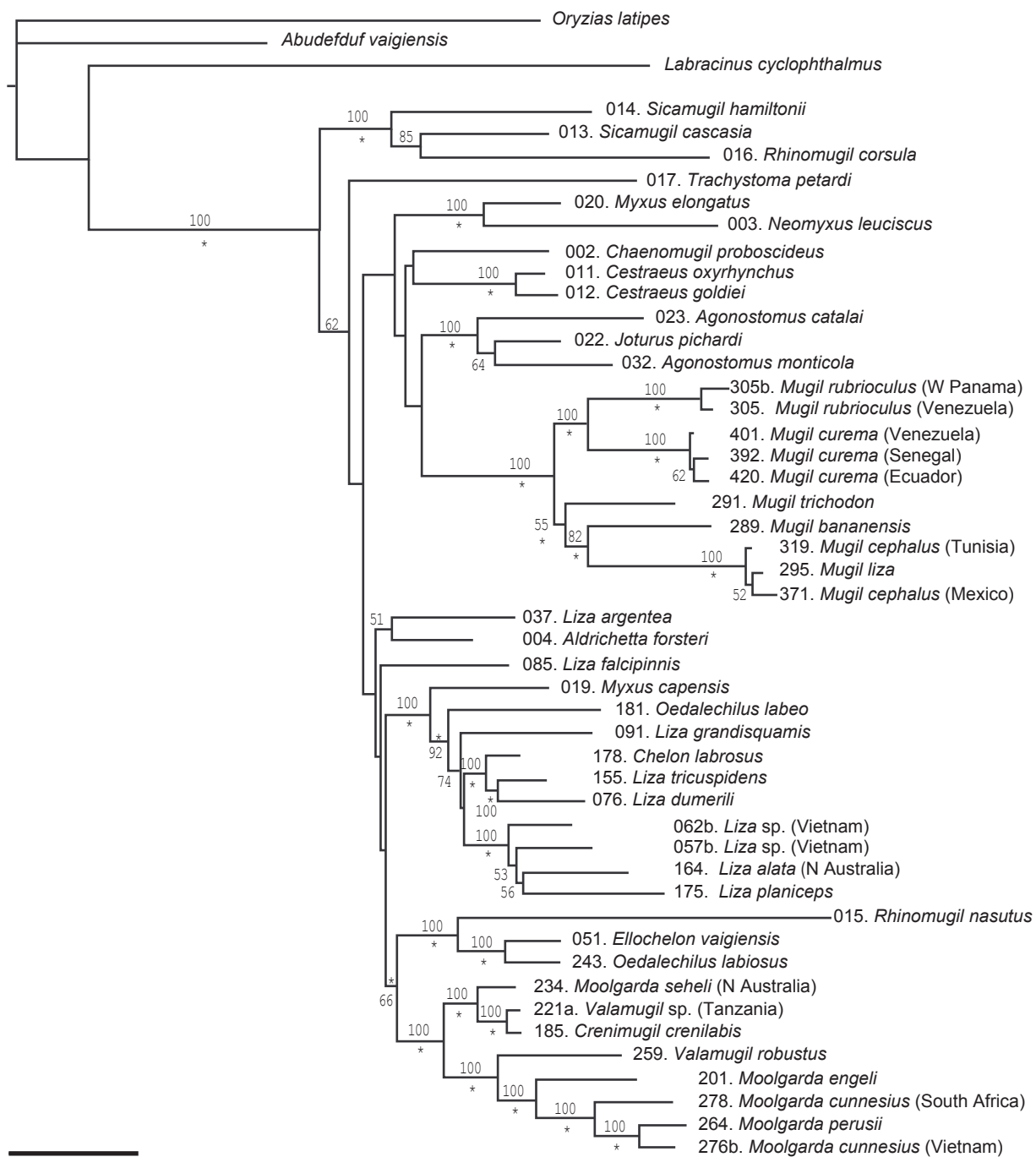


Fig. 2 Durand et al.

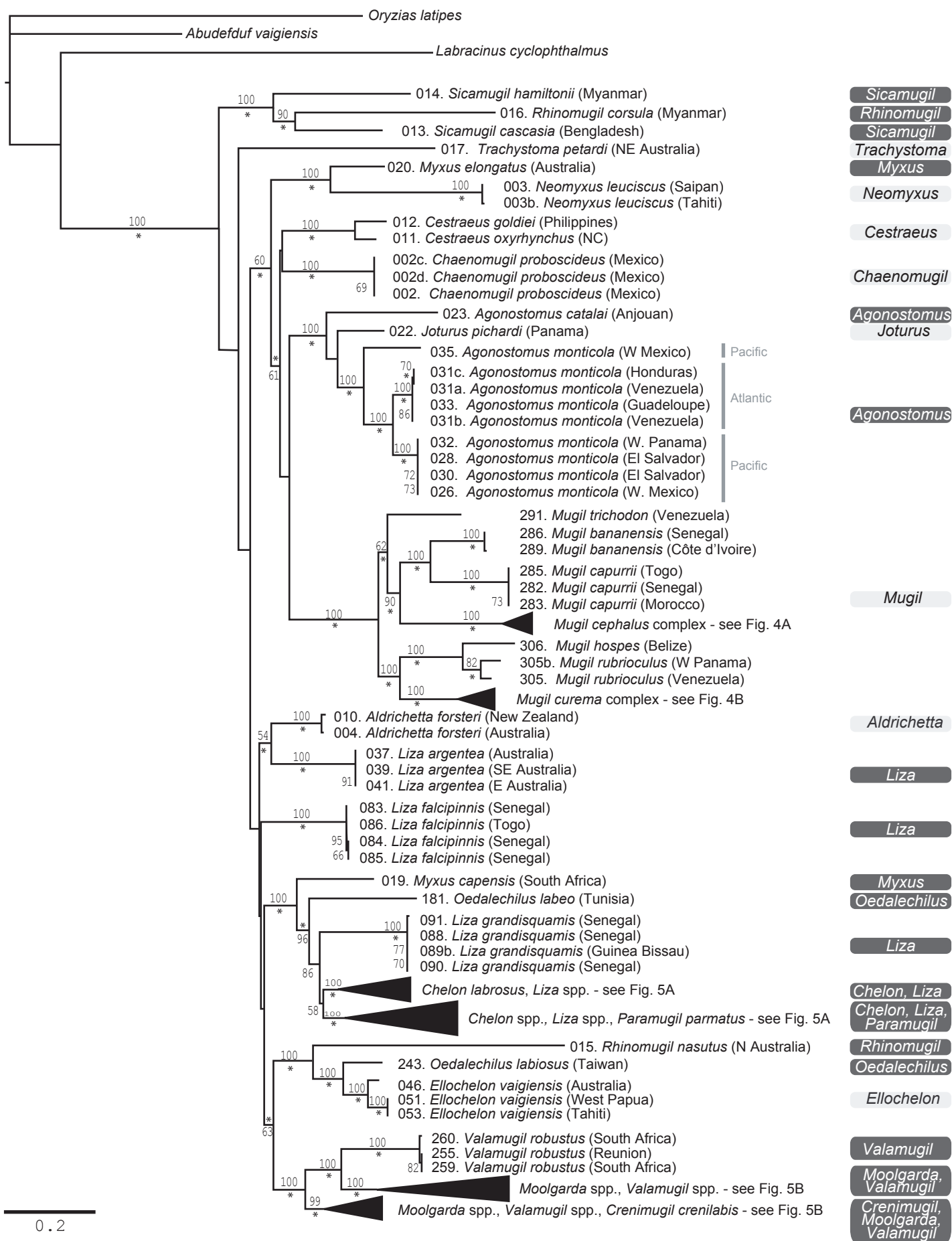
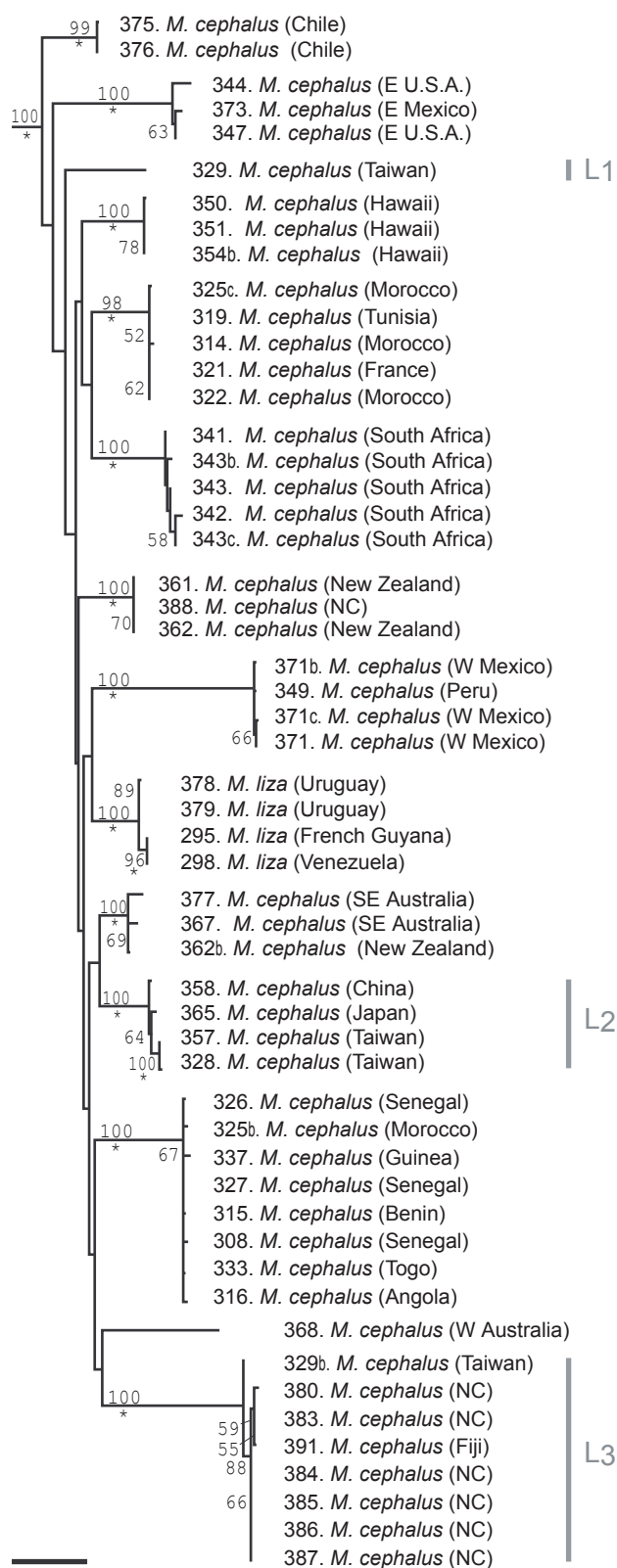


Fig. 3 Durand et al.

A



B

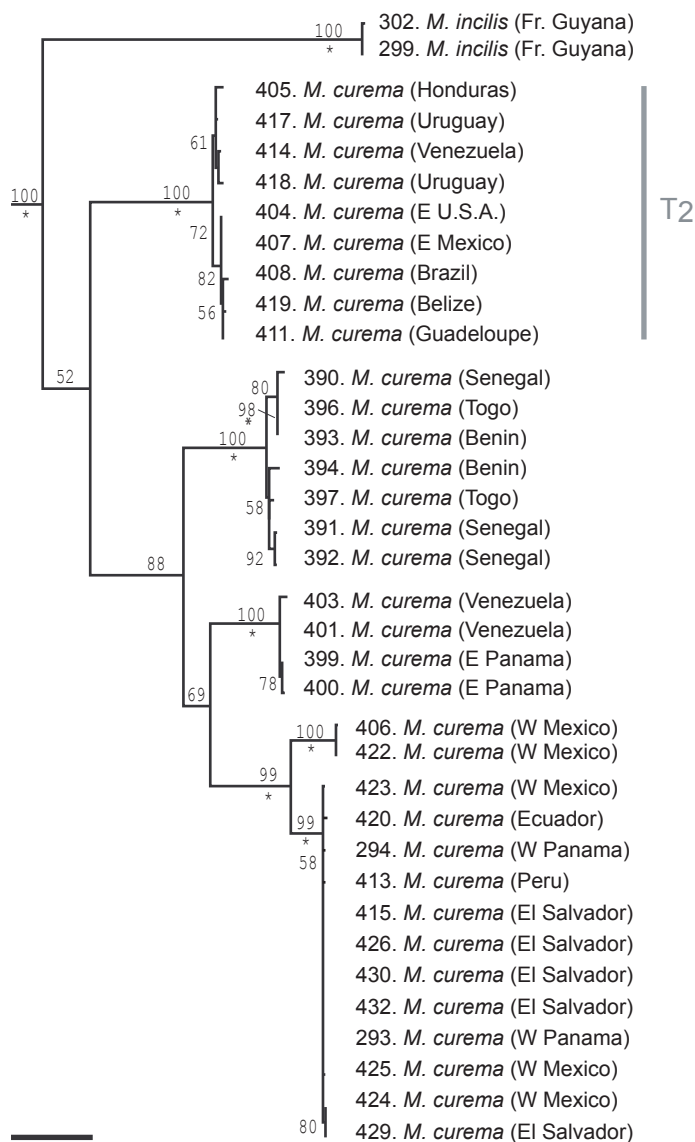
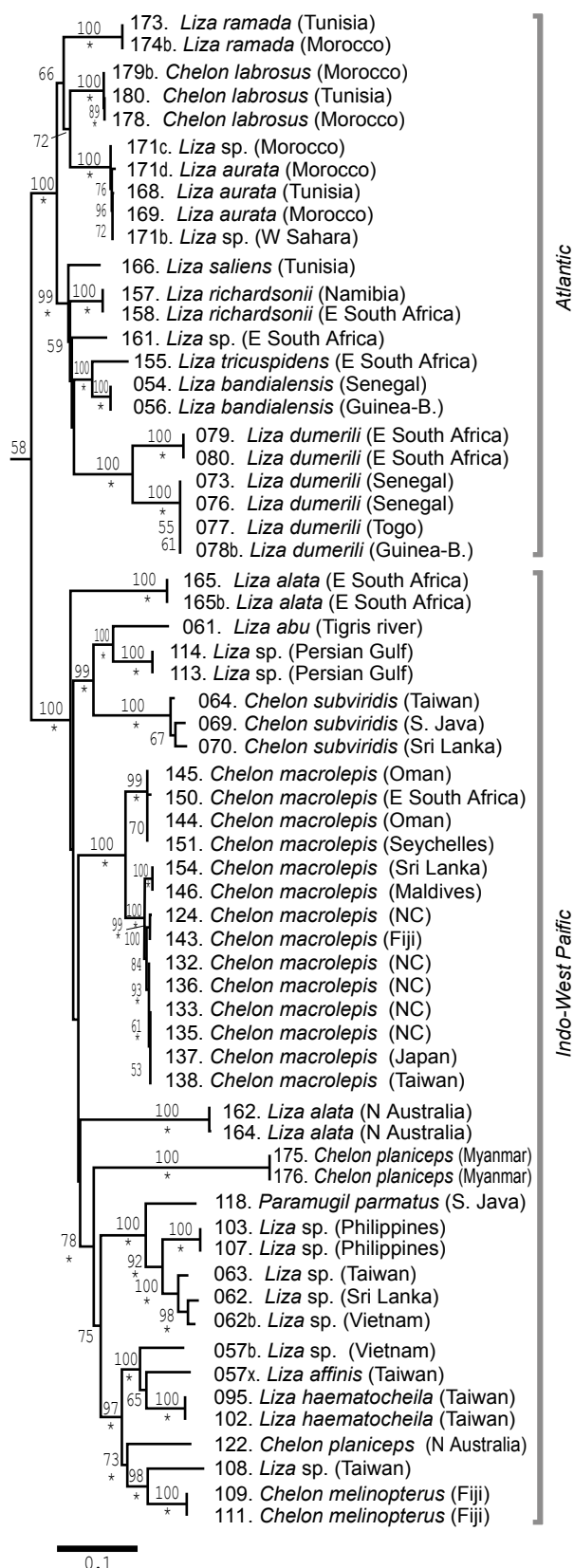


Fig. 4 - Durand et al.

A



B

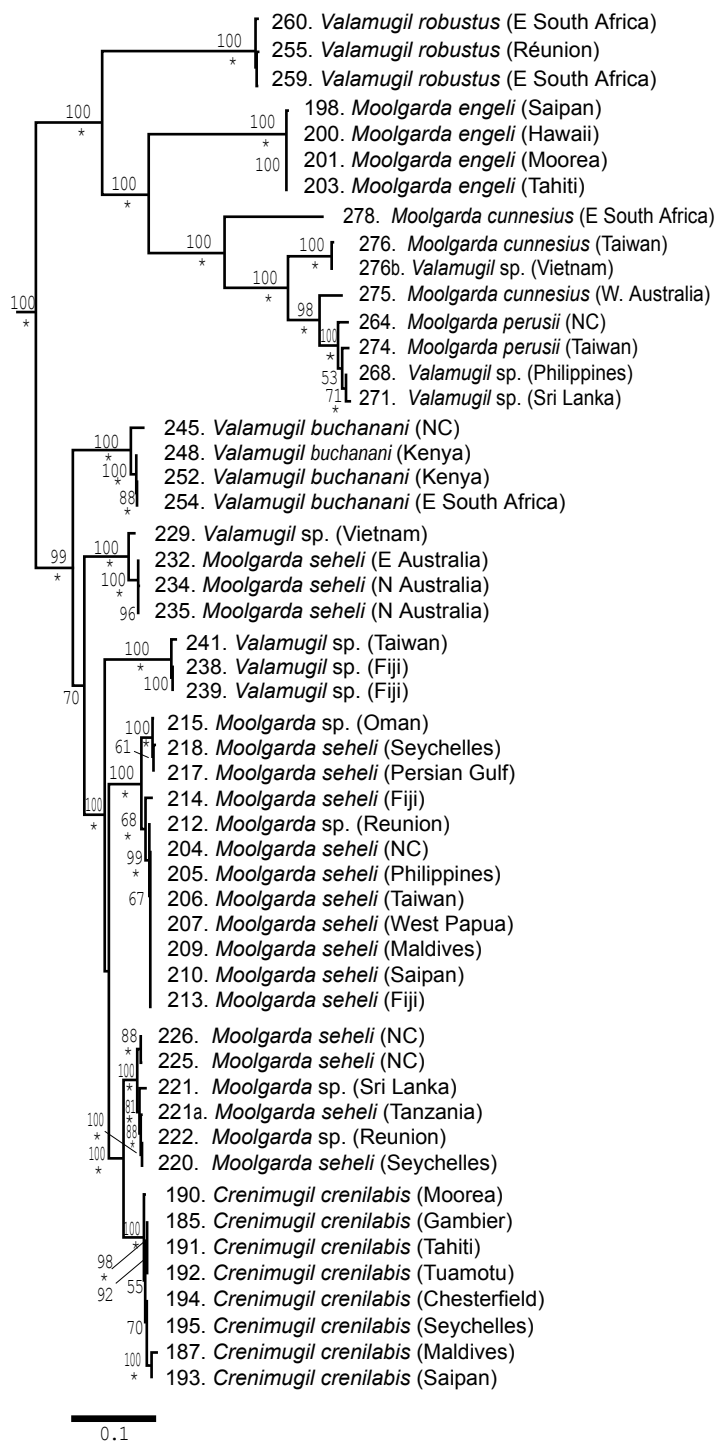


Fig. 5 - Durand et al.