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Taxonomy/Taxinomie

Genus-level taxonomic changes implied by the mitochondrial phylogeny of grey mullets (Teleostei: Mugilidae)

Révision des genres chez les mulets (Teleostei : Mugilidae), consécutive à la phylogénie mitochondriale des espèces de la famille

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ABSTRACT

A comprehensive mitochondrial phylogeny of the family Mugilidae (Durand et al., Mol. Phylogenet. Evol. 64 (2012) 73–92 [1]) demonstrated the polyphyly or paraphyly of a proportion of the 20 genera in the family. Based on these results, here we propose a revised classification with 25 genera, including 15 genera currently recognized as valid (*Agonostomus*, *Aldrichetta*, *Cestraeus*, *Chaenomugil*, *Chelon*, *Crenimugil*, *Ellochelon*, *Joturus*, *Mugil*, *Myxus*, *Neomyxus*, *Oedalechilus*, *Rhinomugil*, *Sicamugil* and *Trachystoma*), 7 resurrected genera [*Dajaus* (for *Agonostomus monticola*), *Gracilimugil* (for *Liza argentea*), *Minimugil* (for *Sicamugil cascasia*), *Osteomugil* (for several species currently under *Moolgarda* and *Valamugil*, including *M. cunnesius*, *M. engeli*, *M. perusii*, and *V. robustus*), *Planiliza* (for Indo-Pacific *Chelon* spp., Indo-Pacific *Liza* spp., and *Paramugil parmatus*), *Plicomugil* (for *Oedalechilus labiosus*), and *Squalomugil* (for *Rhinomugil nasutus*)] and 3 new genera: *Neochelon* gen. nov. (for *Liza falcipinnis*), *Parachelon* gen. nov. (for *L. grandisquamis*) and *Pseudomyxus* gen. nov. (for *Myxus capensis*). Genus *Chelon* was shown to include exclusively *Chelon* spp. and *Liza* spp. from the Atlantic and the Mediterranean, and *Liza* spp. species endemic to eastern southern Africa. Genus *Crenimugil* should now include *C. crenilabis*, *Moolgarda seheli* and *V. buchani*. Genus names *Liza*, *Moolgarda*, *Paramugil*, *Valamugil* and *Xenomugil* should be abandoned because they are no longer valid. Further genetic evidence is required to confirm or infirm the validity of the genus *Paracrenimugil* Senou 1988. The mitochondrial phylogeny of the 25 genera from the present revision is the following: [(*Sicamugil*, (*Minimugil*, *Rhinomugil*)); *Trachystoma*; ((*Myxus*, *Neomyxus*), (*Cestraeus*, *Chaenomugil*, (*Agonostomus*, *Dajaus*, *Joturus*), *Mugil*)); (*Aldrichetta*, *Gracilimugil*); *Neochelon* gen. nov.; (*Pseudomyxus* gen. nov., (*Chelon*, *Oedalechilus*, *Planiliza*, *Parachelon* gen. nov.)); ((*Squalomugil*, (*Ellochelon*, *Plicomugil*)), (*Crenimugil*, *Osteomugil*)). *Agonostomus monticola* and several species with large distribution ranges (including *Moolgarda seheli*, *Mugil cephalus* and *M. curema*) consist of separate lineages whose geographic distribution suggests they are cryptic species, thus warranting further taxonomic work in the Mugilidae at the infra-generic level.

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R É S U M É

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Une phylogénie mitochondriale complète des Mugilidae (Durand et al., Mol. Phylogenet. Evol. 64 (2012) 73–92 [1]) a démontré la polyphylie ou la paraphylie d'une partie des 20 genres de cette famille. D'après ces résultats, nous proposons ici une classification révisée avec 25 genres, qui comprend 15 genres actuellement reconnus comme valides (*Agonostomus*, *Aldrichetta*, *Cestraeus*, *Chaenomugil*, *Chelon*, *Crenimugil*, *Ellochelon*, *Joturus*, *Mugil*, *Myxus*, *Neomyxus*, *Oedalechilus*, *Rhinomugil*, *Sicamugil* et *Trachystoma*), 7 genres réhabilités [*Dajaus* (pour *Agonostomus monticola*), *Gracilimugil* (pour *Liza argentea*), *Minimugil* (pour *Sicamugil cascasia*), *Osteomugil* (pour plusieurs espèces des genres *Moolgarda* et *Valamugil*, dont *M. cunnesius*, *M. engeli*, *M. perusii* et *V. robustus*), *Planiliza* (pour les espèces indo-pacifiques des genres *Chelon* et *Liza* ainsi que *Paramugil parmatus*), *Plicomugil* (pour *Oedalechilus labiosus*) et *Squalomugil* (pour *Rhinomugil nasutus*)] et 3 nouveaux genres : *Neochelon* gen. nov. (pour *Liza falcipinnis*), *Parachelon* gen. nov. (pour *L. grandisquamis*) et *Pseudomyxus* gen. nov. (pour *Myxus capensis*). Nous proposons que le genre *Chelon* comprenne désormais *C. labrosus* et tous les *Liza* spp. de l'Atlantique et de la Méditerranée ainsi que les *Liza* spp. endémiques de l'Afrique du Sud. Le genre *Crenimugil* doit désormais inclure *C. crenilabis*, *Moolgarda seheli* et *V. buchanani*. Les noms de genres *Liza*, *Moolgarda*, *Paramugil*, *Valamugil* et *Xenomugil*, non valides, doivent être abandonnés. Des analyses génétiques supplémentaires sont requises pour confirmer ou infirmer la validité du genre *Paracrenimugil* Senou 1988. La phylogénie mitochondriale des 25 genres ainsi proposés est la suivante : [(*Sicamugil*, (*Minimugil*, *Rhinomugil*)); *Trachystoma*; ((*Myxus*, *Neomyxus*), (*Cestraeus*, *Chaenomugil*, (*Agonostomus*, *Dajaus*, *Joturus*), *Mugil*)) ; (*Aldrichetta*, *Gracilimugil*) ; *Neochelon* gen. nov. ; (*Pseudomyxus* gen. nov., (*Chelon*, *Oedalechilus*, *Planiliza*, *Parachelon* gen. nov.)) ; ((*Squalomugil*, (*Ellochelon*, *Plicomugil*)), (*Crenimugil*, *Osteomugil*)). *Agonostomus monticola* et plusieurs espèces à large distribution géographique (y compris les espèces *Moolgarda seheli*, *Mugil cephalus* et *M. curema*) se composent de lignées distinctes dont la répartition géographique suggère l'existence d'espèces cryptiques, justifiant ainsi de nouvelles recherches sur la taxonomie des Mugilidae au niveau infra-générique.

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1. Introduction

The potential input of molecular phylogenies to modern taxonomy is considerable [2–5], to the extent that a DNA-based approach to taxonomy is being envisaged [6–8]. It is arguable that molecular phylogenies should provide the basis to taxonomy in the cases where conflicts or uncertainty persist from classifications based on morphology, morpho-anatomy, and other phenotypic characters. Unlike molecular phylogenies, traditional taxonomy based on morphological characters can for instance be misled by phenotypic plasticity, morphological convergence, and arbitrary character weighting [8,9].

In the last 130 years, up to 281 nominal species and 43 nominal genera (Table 1) have been proposed for the Mugilidae [11]. The first thorough taxonomic revision of the Mugilidae was produced by Schultz [38], who mainly used mouth anatomy to define species and genera. Schultz [38] validated only ten previously defined mugilid genera and described three new ones, a revision that was subsequently questioned (review in [43]). The taxonomy and nomenclature of Mugilidae have still not been finalized [44], with between 14 and 20 genera being recognized as valid according to the most recent revisions [11,12,45]. The Integrated Taxonomic Information System (<http://www.itis.gov/>; information retrieved on 16 August 2011) recognizes 16 valid genera, while Eschmeyer and Fricke [13] list 20 valid genera. Two genera, *Liza* and *Mugil*, currently represent 40% of the species richness of the

family Mugilidae [13]. While the taxonomy and nomenclature of species in the genus *Mugil* are mostly stable, those in the genus *Liza* have undergone changes since [38] (Table 1), reflecting disagreement among authors regarding the taxonomic placement of some of the species currently under this genus.

Molecular phylogenetic investigations of the Mugilidae have been mostly regional in scope, with a majority of studies concerning mugilid species sampled from the Mediterranean region, and a few other studies concerned with species from the Atlantic waters of South America, or from India, or from eastern Asia (reviewed in [1]). More recent studies have attempted to expand taxonomic sampling by including species and genera from various locations worldwide in addition to their initial treatment of Mediterranean Mugilidae [46,47]. The most comprehensive phylogenetic survey of Mugilidae published thus far concerned 55 species representing 19 of the 20 currently recognized genera [1] (Fig. 1). A substantial proportion of the species in particularly speciose genera *Chelon* (5/7 of currently recognized species), *Liza* (14/19), *Mugil* (9/12), *Moolgarda* (4/5) and *Valamugil* (3/4) were included. Broad geographic sampling was undertaken for the ubiquitous genera *Chelon*, *Liza*, and *Mugil*. Emphasis was also put on sampling several widely-distributed species of these and other genera, including *C. macrolepis*, *Crenimugil crenilabis*, *Moolgarda cunnesius*, *M. seheli*, *Mugil cephalus*, *M. curema* and *Valamugil buchanani*.

Table 1

Nominal genera of the Mugilidae in chronological order of appearance, with their status according to Senou [10], Thomson [11], Ghasemzadeh [12], Eschmeyer and Fricke [13] and this study.

Genus	Author and date	Ref.	Type species	Genus assigned by author (date)				
				Senou (1988)	Thomson (1997)	Ghasemzadeh (1998)	Eschmeyer and Fricke (2011)	This study
<i>Mugil</i>	Linnaeus 1758	[14]	<i>Mugil cephalus</i> Linnaeus 1758	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>
<i>Chelon</i>	Artedi 1793	[15]	<i>Mugil chelo</i> Cuvier 1829	<i>Chelon</i>	<i>Chelon</i>	<i>Chelon</i>	<i>Chelon</i>	<i>Chelon</i>
<i>Cephalus</i>	Lacepède 1799	[16]	<i>Mugil cephalus</i> Linnaeus 1758	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>
<i>Agonostomus</i>	Bennett 1832	[17]	<i>Agonostomus telfairii</i> Bennett 1832	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>
<i>Cestraeus</i>	Valenciennes 1836	[18]	<i>Cestraeus plicatilis</i> Valenciennes 1836	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>
<i>Dajaus</i>	Valenciennes 1836	[18]	<i>Mugil monticola</i> Bancroft 1834	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Dajaus</i>
<i>Nestis</i>	Valenciennes 1836	[18]	<i>Nestis cyprinoidea</i> Valenciennes 1836	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>
<i>Arnion</i>	Gistel 1848	[19]	<i>Mugil cephalus</i> Linnaeus 1758	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>
<i>Ello</i>	Gistel 1848	[19]	<i>Mugil cephalus</i> Linnaeus 1758	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>
<i>Joturus</i>	Poey 1860	[20]	<i>Joturus pichardi</i> Poey 1860	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>
<i>Myxus</i>	Günther 1861	[21]	<i>Myxus elongatus</i> Günther 1861	<i>Chelon</i>	<i>Myxus</i>	<i>Myxus</i>	<i>Myxus</i>	<i>Myxus</i>
<i>Chaenomugil</i>	Gill 1863	[22]	<i>Mugil proboscideus</i> Günther 1861	<i>Chaenomugil</i>	<i>Chaenomugil</i>	<i>Chaenomugil</i>	<i>Chaenomugil</i>	<i>Chaenomugil</i>
<i>Rhinomugil</i>	Gill 1863	[22]	<i>Mugil corsula</i> Hamilton 1822	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>
<i>Gonostomyxus</i>	Macdonald 1869	[23]	<i>Gonostomyxus loaloa</i> Macdonald 1869	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>
<i>Neomyxus</i>	Steindachner 1878	[24]	<i>Myxus (Neomyxus) sclateri</i> Steindachner 1878	<i>Neomyxus</i>	<i>Chaenomugil</i>	<i>Neomyxus</i>	<i>Neomyxus</i>	<i>Neomyxus</i>
<i>Querimana</i>	Jordan and Gilbert 1883	[25]	<i>Myxus harengus</i> Günther 1861	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>
<i>Aeschrithys</i>	Macleay 1883	[26]	<i>Aeschrithys goldiei</i> Macleay 1883	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>	<i>Cestraeus</i>
<i>Liza</i>	Jordan and Swain 1884	[27]	<i>Mugil capito</i> Cuvier 1829	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>
<i>Trachystoma</i>	Ogilby 1888	[28]	<i>Trachystoma multidens</i> Ogilby 1888	<i>Chelon</i>	<i>Myxus</i>	<i>Trachystoma</i>	<i>Trachystoma</i>	<i>Trachystoma</i>
<i>Neomugil</i>	Vaillant 1894	[29]	<i>Neomugil digueti</i> Vaillant 1894	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Dajaus</i>
<i>Oedalechilus</i>	Fowler 1903	[30]	<i>Mugil labeo</i> Cuvier 1829	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>
<i>Squalomugil</i>	Ogilby 1908	[31]	<i>Mugil nasutus</i> de Vis 1883	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Squalomugil</i>
<i>Xenorhynchichthys</i>	Regan 1908	[32]	<i>Joturus stipes</i> Jordan and Gilbert 1882	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>
<i>Ellochelon</i>	Whitley 1930	[33]	<i>Mugil vaigiensis</i> Quoy and Gaimard 1825	<i>Ellochelon</i>	<i>Liza</i>	<i>Ellochelon</i>	<i>Ellochelon</i>	<i>Ellochelon</i>
<i>Protomugil</i>	Popov 1930	[34]	<i>Mugil saliens</i> Risso 1810	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>
<i>Sicamugil</i>	Fowler 1939	[35]	<i>Mugil hamiltoni</i> Day 1869	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>
<i>Gracilimugil</i>	Whitley 1941	[36]	<i>Mugil ramsayi</i> Macleay 1883	<i>Chelon</i>	<i>Liza</i>	<i>Gracilimugil</i>	<i>Liza</i>	<i>Gracilimugil</i>
<i>Moolgarda</i>	Whitley 1945	[37]	<i>Moolgarda pura</i> Whitley 1945	<i>Moolgarda</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Moolgarda</i>	-
<i>Planiliza</i>	Whitley 1945	[37]	<i>Moolgarda (Planiliza) ordensis</i> Whitley 1945	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>
<i>Aldrichetta</i>	Whitley 1945	[37]	<i>Mugil forsteri</i> Valenciennes 1836	<i>Aldrichetta</i>	<i>Aldrichetta</i>	<i>Aldrichetta</i>	<i>Aldrichetta</i>	<i>Aldrichetta</i>
<i>Xenomugil</i>	Schultz 1946	[38]	<i>Mugil thoburni</i> Jordan and Starks 1896	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Xenomugil</i>	<i>Mugil</i>
<i>Crenimugil</i>	Schultz 1946	[38]	<i>Mugil crenilabis</i> Forsskål 1775	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>
<i>Heteromugil</i>	Schultz 1946	[38]	<i>Mugil tricuspiciens</i> Smith 1935	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>	<i>Chelon</i>
<i>Oxymugil</i>	Whitley 1948	[39]	<i>Mugil acutus</i> Valenciennes 1836	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>
<i>Pteromugil</i>	Smith 1948	[40]	<i>Mugil diadema</i> Gilchrist and Thompson 1911	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>
<i>Strializa</i>	Smith 1948	[40]	<i>Mugil canaliculatus</i> Smith 1935	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>
<i>Valamugil</i>	Smith 1948	[40]	<i>Mugil seveli</i> Forsskål 1775	<i>Moolgarda</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Crenimugil</i>
<i>Plicomugil</i>	Schultz 1953	[41]	<i>Mugil labiosus</i> Valenciennes 1836	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Plicomugil</i>
<i>Osteomugil</i>	Lüther 1977	[42]	<i>Mugil cunnesius</i> Valenciennes 1836	<i>Moolgarda</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Osteomugil</i>
<i>Minimugil</i>	Senou 1988	[10]	<i>Mugil casasia</i> Hamilton 1822	<i>Minimugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Minimugil</i>
<i>Paracrenimugil</i>	Senou 1988	[10]	<i>Mugil heterocheilus</i> Bleeker 1855	<i>Paracrenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	ND
<i>Pseudoliza</i>	Senou 1988	[10]	<i>Mugil parmatus</i> Cantator 1849	<i>Pseudoliza</i>	<i>Liza</i>	<i>Paramugil</i>	<i>Paramugil</i>	<i>Planiliza</i>
<i>Paramugil</i>	Ghasemzadeh 1998	[12]	<i>Mugil parmatus</i> Cantator 1849	<i>Pseudoliza</i>	<i>Valamugil</i>	<i>Paramugil</i>	<i>Paramugil</i>	<i>Planiliza</i>
-	-	-	<i>Mugil falcipinnis</i> Valenciennes 1836	<i>Chelon</i>	<i>Liza</i>	-	<i>Liza</i>	<i>Neochelon</i> gen. nov.
-	-	-	<i>Mugil grandisquamis</i> Valenciennes 1836	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Liza</i>	<i>Parachelon</i> gen. nov.
-	-	-	<i>Mugil capensis</i> Valenciennes 1836	<i>Chelon</i>	<i>Myxus</i>	<i>Myxus</i>	<i>Myxus</i>	<i>Pseudomyxus</i> gen. nov.

ND: no data.

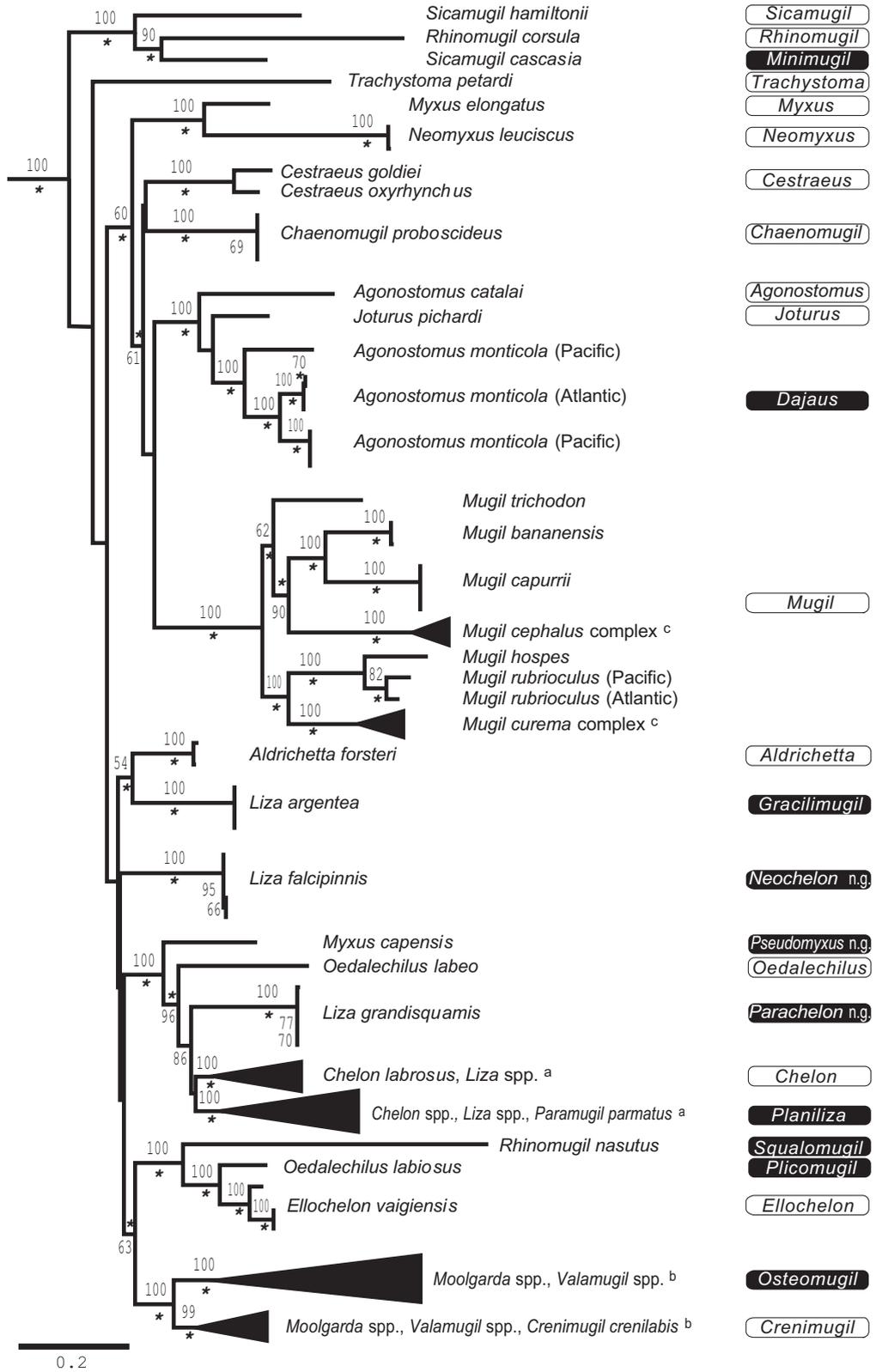


Fig. 1. Revised genus names in Mugilidae, superimposed on the phylogenetic tree of Mugilidae (55 species from 19 genera) inferred using partitioned maximum-likelihood analysis of 3885 aligned nucleotides from three mitochondrial gene loci (modified from [1]). Taxon names at extremity of branches according to the current nomenclature [13]; when species identification was uncertain, an unknown species or "sp." was assigned to the recognized genus

Durand et al.'s [1] phylogeny allowed one to test previous phylogenetic hypotheses based on morphology and morphoanatomy, themselves in contradiction with one another (Fig. 1A–E of [1]). It was found that several genera in the Mugilidae actually were polyphyletic or paraphyletic and that the molecular phylogeny matches no one of the previous, morphology-based classifications. Here, we propose a revised classification based on these results.

2. Methods

We thus examined the phylogenetic placement of each of the 19 mugilid genera in the mitochondrial phylogeny of Mugilidae produced by [1] (Fig. 1). In addition, we determined the phylogenetic placement of the genus *Xenomugil* (represented by its single species *X. thoburni*).

A partial phylogeny of Mugilidae based on all available nucleotide sequences of a 300-bp fragment of the cytochrome *b* (*cytb*) gene had initially shown *X. thoburni* haplotypes to be embedded within the *Mugil curema* lineage (Appendix A). Consequently, here we run a new phylogenetic analysis (following procedures described in [1]) of the genera *Mugil* and *Xenomugil*, using a new matrix of sequences that comprised representatives from all *Mugil* spp. lineages of [1], the new sequences of two *X. thoburni* individuals, and the additional sequences of two *M. cephalus* individuals from the Galapagos Islands. Both *X. thoburni* and additional *M. cephalus* from the Galapagos Islands were collected at Bahia Divine, Isla Santa Cruz on 15 June 2011 by T. Ballesteros. Their partial nucleotide sequences at the 16S rRNA (16S), cytochrome-oxidase I (*COI*) and *cytb* loci [GENBANK (<http://www.ncbi.nlm.nih.gov>) accession numbers JX559523 to JX559535] were obtained using the same experimental protocols as [1].

For the present revision, a genus name was conserved if the topology of the tree supported the monophyly of the genus. When a genus currently considered valid was paraphyletic or polyphyletic, we split it into the minimum necessary number of genera according to the topology of the tree. The current genus name was conserved for the type species (Table 1) and, when applicable, its sister species in the same genus. For the other monophyletic groups under the same genus, former genus names were resurrected whenever applicable. For this, we considered the history of genus nomenclature in Mugilidae and the validity of the 43 genera proposed thus far (Table 1). The principle of priority [51] was followed when a previously proposed genus name was available. When no genus name was available for a given lineage, we proposed a new genus name.

Thus, our concern was to minimize disruption to the existing nomenclature. This accords with the principles of the PhyloCode [52].

3. Results and discussion

A summary of Durand et al.'s [1] phylogenetic results (Fig. 1) and their taxonomic implications at the genus level are examined in the following. We added information on the distribution of each genus. Genera are listed in alphabetical order.

3.1. *Agonostomus*

Agonostomus was paraphyletic with respect to *Joturus*; *A. monticola* was phylogenetically closer to *J. pichardi* than both were from *A. catalai* (Fig. 1). At locus 16S, the nucleotide divergence between *A. monticola* (GENBANK JQ060644–JQ060652) and *A. catalai* (GENBANK JQ060643) was 13.3–13.5% (Kimura 2-parameter; MEGA 5 [49]) while the estimated divergence between *A. telfairii* (GENBANK DQ532834) and *A. catalai* was 0.2%. Since *A. telfairii*, which is the type-species of the genus, is genetically closer to *A. catalai* than *A. monticola*, it is the latter that should be placed under a different genus name, namely *Dajaus* which is the earliest genus name available for *A. monticola* (Table 1). The genus *Agonostomus* under its present, revised definition exclusively occurs in the South-West Indian Ocean [11].

3.2. *Aldrichetta*

Aldrichetta was found to be the sister subclade of *Liza argentea*; no taxonomic change is needed for *Aldrichetta*, which is monotypic [13]. The distribution of this genus is restricted to the temperate coastal waters of Australia and New Zealand [11].

3.3. *Cestraeus*

The genus *Cestraeus*, represented by two species (*C. goldiei* and *C. oxyrhinchus*) in [1] was found to be monophyletic and a brother genus to *Chaenomugil*, *Mugil*, and (*Agonostomus* + *Joturus*); no taxonomic change is needed regarding *Cestraeus* because of its monophyly. The genus *Cestraeus* is present in the Indo-Malay-Papua archipelago, in New Caledonia and in Fiji [11].

3.4. *Chaenomugil*

This genus was found to be a brother genus to *Cestraeus*, *Mugil* and (*Agonostomus* + *Joturus*). No taxonomic change is needed for *Chaenomugil*, which is monotypic [13]. *C. proboscideus*, the only species in the genus, occurs in the eastern Pacific, from Baja California to Peru [11].

3.5. *Chelon*

Chelon labrosus grouped with *L. aurata*, *L. ramada*, *L. saliens*, *L. richardsonii*, *L. bandialensis*, *L. dumerili*, *Liza* sp.

for the taxon. Proposed new genus designations are shown on the right-hand side of the figure; *black background*: resurrected genera or newly proposed genera ('n.g.'): *open*: genera maintained in their current name. 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 [1]; *scale bar*: 0.1 inferred nucleotide substitution/site under (GTR + G + I) model. ^a Details in Fig. 2A; ^b details in Fig. 2b; ^c details in Fig. 2C.

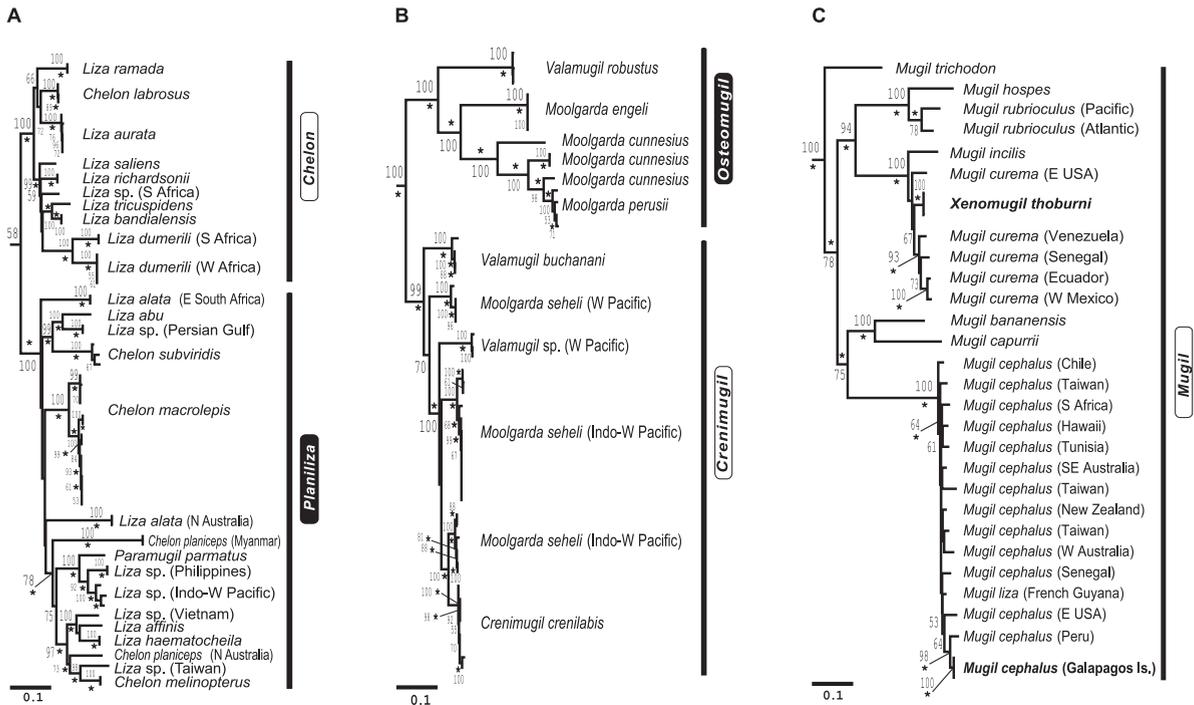


Fig. 2. Details of the tree presented in Fig. 1. Taxon names at extremity of branches are given according to the current nomenclature [13]; when species identification was uncertain, an unknown species or “sp.” was assigned to the recognized genus for the taxon. Proposed new genus designations are shown on the right-hand side of each figure; **black background**: resurrected genera; **open**: genera maintained in their current name. 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 [1]; *scale bars*: 0.1 inferred nucleotide substitution/site. A. Revised genus names proposed for species in the current genera *Chelon*, *Liza* and *Paramugil*. B. Revised genus names proposed for the current genera *Crenimugil*, *Moolgarda* and *Valamugil*. C. Phylogenetic tree depicting relationships of *Mugil* spp. and *Xenomugil thoburni*. Relationships were inferred using partitioned maximum-likelihood (RAXML [53]) analysis of 2,385 aligned nucleotides from partial 16S, *COI* and *cytb* genes (ML score - 13535.1). *Myxus elongatus* and *Agonostomus catalai* were selected as outgroup taxa following the mugilid phylogeny of [1] (Fig. 1). Branch lengths are proportional to number of substitutions under the (GTR + G) model. **Bold**: taxa not included in [1].

(S. Africa) and *L. tricuspidens* to form a subclade (Fig. 2A), which turned out to exclusively comprise species distributed in Atlantic and Mediterranean waters or species apparently endemic to eastern southern Africa (*L. tricuspidens*, *L. richardsonii* and an apparently undescribed *Liza* sp. [1]). The other *Chelon* species sampled, all from the Indo-Pacific, formed a distinct subclade together with Indo-Pacific *Liza* spp. and *Paramugil parmatus*. All species in the ‘Atlantic’ subclade (Fig. 5A of [1]), which includes *Chelon labrosus* (the type species of the genus *Chelon*) should be placed under *Chelon* by the principle of priority (Table 1). The other *Liza* and *Chelon* species sampled should be placed under different genera (see below).

3.6. *Crenimugil*

Crenimugil crenilabis (the type species of the genus *Crenimugil*; Table 1) grouped with *Moolgarda seheli* and *Valamugil buchanani* to form a distinct cluster within the (*Crenimugil*, *Moolgarda*, *Valamugil*) subclade (Fig. 2B). This well-supported lineage should be named *Crenimugil* because of the priority of the latter to *Valamugil* (Table 1), and because *Moolgarda* is both a nomen nudum and a nomen dubium [11]. The close evolutionary affinity of

C. crenilabis with *M. seheli* and *V. buchanani* has previously been highlighted on the basis of shared morpho-anatomical characters ([10]; Fig. 3). We were unable to obtain a sample of *C. heterocheilos*, designated by Senou [10] as the type species of his genus *Paracrenimugil*. Based on the accuracy of the rest of Senou’s [10] cladistic tree (Fig. 3), resurrecting the genus *Paracrenimugil* for *C. heterocheilos* is an eventuality that deserves consideration. The genus *Crenimugil* has a wide Indo-West Pacific distribution.

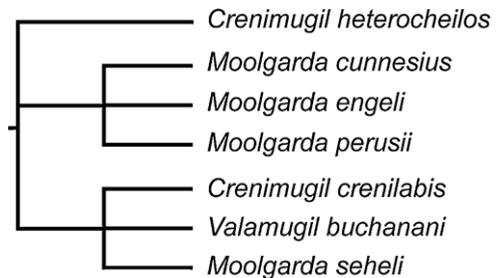


Fig. 3. Parsimony tree of *Moolgarda* spp., *Valamugil buchanani* and *Crenimugil* spp. based on a cladistic analysis of 46 morphological characters (redrawn from [10]).

3.7. *Ellochelon*

The genus *Ellochelon* was found to be the sister lineage of *Oedalechilus labiosus*. No taxonomic change is needed for *Ellochelon*, which is monotypic [13]. *E. vaigiensis* has a wide Indo-West Pacific distribution, from Natal to Tahiti [11].

3.8. *Joturus*

The genus *Joturus* was the sister lineage of *Agonostomus monticola*. No taxonomic change is needed for *Joturus*, which is monotypic [13]. This genus is present on both the Pacific and the Atlantic coasts of the American continent, from Mexico to Panama, and in the Caribbean Sea [11].

3.9. *Liza*

The type species of the genus *Liza* is *Mugil capito* (currently *L. ramada*; [13]). The phylogenetic results of [1] imply that *L. ramada* be placed under genus *Chelon*, which in turn implies that *Liza* is a junior synonym of *Chelon*. Hence, the name *Liza* is now unavailable.

Liza argentea and *L. falcipinnis* were each distinct from the other *Liza* species, all of which clustered within a single clade (Fig. 1). 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 above), and a third sub-clade that includes *Chelon* spp. and *Liza* spp. from the Indo-West Pacific only (namely, *C. macrolepis*, *C. melinopterus*, *C. planiceps*, *C. subviridis*, *L. abu*, *L. affinis*, *L. alata*, *L. haematocheila*, and *Paramugil parmatus*) (Fig. 2A). *Liza argentea* and *L. falcipinnis* each merit an individual genus name. *Liza argentea* was previously assigned to the genus *Gracilimugil* [36] and we here propose that this genus be resurrected for this species; *L. falcipinnis* should be assigned a new genus name since there does not seem to be any genus name available for that species (Table 1), and *L. grandisquamis* should similarly be assigned a new genus name [51]. The 'Indo-West Pacific' (*Chelon* spp. + *Liza* spp. + *P. parmatus*) subclade contains *L. alata*, a senior synonym of *L. ordensis* which is the type species of the subgenus *Planiliza* [37] (Table 1), hence it should be assigned genus name *Planiliza* by the principle of priority [51]. The genus *Gracilimugil* occurs in southwestern Australia.

3.10. *Moolgarda*

This genus was polyphyletic (Figs. 1 and 2B). The name *Moolgarda* predates both *Crenimugil* and *Valamugil* (Table 1) but the position of *M. pura*, the type species of the genus [37], is uncertain and the type specimen has been lost [11]. Therefore, *Moolgarda* should be considered a nomen dubium and no use can be made of this genus name in the present revision. The *Moolgarda* species that belong to the *Crenimugil crenilabis* subclade should be placed under *Crenimugil* (see above). The other species, including *M. cunnesius*, *M. engeli*, *M. perusii* and *Valamugil robustus* clustered into a distinct subclade (Fig. 2B), hence deserve a

different genus name. For this, we propose to use the name *Osteomugil* following Lüther [42], who described this genus from *M. cunnesius* (the type species), and who also suggested that it might include *M. engeli*.

3.11. *Mugil*

All 9 *Mugil* species examined by [1] (*M. bananensis*, *M. capurrii*, *M. cephalus*, *M. curema*, *M. hospes*, *M. incilis*, *M. liza*, *M. rubrioculus* and *M. trichodon*) clustered into a single, well-supported clade (Fig. 4A of [1]). *Mugil* was found to be paraphyletic with *Xenomugil* (Fig. 2C). The name *Mugil* remains valid by the principle of priority [51] (Table 1). This genus has a temperate-tropical circumglobal distribution [11].

3.12. *Myxus*

Myxus was 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. The name *Myxus* should be maintained for *M. elongatus* (the type-species of the genus), while *M. capensis* deserves genus rank. As there is currently no genus name available for *M. capensis* (Table 1), a new genus name has to be proposed. The genus *Myxus* under its present, revised definition is restricted to the temperate waters of Australia.

3.13. *Neomyxus*

Neomyxus is the sister lineage of *M. elongatus*. No taxonomic change is needed for *Neomyxus*, which is monotypic [13]. The only representative of this genus, *N. leuciscus*, occurs around islands of the Central Pacific, from Southern Japanese and Hawaiian islands to Samoa [11].

3.14. *Oedalechilus*

The mitochondrial phylogeny (Fig. 1) revealed a polyphyletic *Oedalechilus*: *O. labeo*, its type species, clustered with *Myxus capensis*, *Chelon* spp., *Liza* spp. and *P. parmatus* to form a distinct subclade, while *O. labiosus* paired with *E. vaigiensis* within another subclade that also included *R. nasutus*. The genus name *Oedalechilus* should be maintained for *O. labeo* (its type-species; Table 1), *O. labiosus* should be reassigned to the genus *Plicomugil* following Schultz [41] and Harrison and Howes [54]. Therefore, under its present, revised definition, the genus *Oedalechilus* is monotypic. It occurs in the Western Mediterranean Sea and in the Azores archipelago [11]. The genus *Plicomugil* is distributed in the Indo-West Pacific, from the Red Sea to the Philippines [11].

3.15. *Paramugil*

Ghasemzadeh [12] defined the genus *Paramugil* for *P. parmatus*, which was embedded within the Indo-Pacific sub-clade of (*Liza* spp. + *Chelon* spp.) (Fig. 2A), for which we argued that the genus name *Planiliza* be resurrected (see

above). Hence, *Paramugil* should now be regarded as a junior synonym of *Planiliza*.

3.16. *Rhinomugil*

Rhinomugil was polyphyletic, with *R. corsula* being the sister lineage of *Sicamugil cascasia*, while *R. nasutus* paired with the lineage that includes *Ellochelon* and *O. labiosus* (Fig. 1). The name *Rhinomugil* should be maintained for *R. corsula*, its type species (Table 1) but *R. nasutus* should be assigned a different genus name, namely *Squalomugil* [31] (Table 1). *R. corsula* is a freshwater species from India; *R. nasutus* occurs in the estuarine waters and mangroves of New Guinea and tropical Australia [11].

3.17. *Sicamugil*

Sicamugil was paraphyletic, with *S. hamiltonii* being sister group to (*R. corsula* + *S. cascasia*) (Fig. 1). *Sicamugil* should be maintained for *S. hamiltonii*, the type species of the genus (Table 1), and *S. cascasia* should be re-assigned to Senou's [10] *Minimugil* (Table 1). *S. hamiltonii* occurs in Myanmar; *S. cascasia* is distributed in the Ganges River and its tributaries [11].

3.18. *Trachystoma*

Genus *Trachystoma* formed a distinct clade on its own. The mitochondrial phylogeny confirmed the peculiar systematic status of the monotypic genus *Trachystoma* (Fig. 1). *T. petardi*, the only species in the genus, inhabits the rivers of eastern Australia, from Queensland to New South Wales [11].

3.19. *Valamugil*

Most *Valamugil* species, along with *Moolgarda* species, were split into two strongly supported lineages, one of which was paraphyletic with *Crenimugil crenilabis*. *V. robustus* belonged to another subclade, which also comprised *Moolgarda* spp. and *Valamugil* spp. *Valamugil* should now be considered as a junior synonym of *Crenimugil* since *V. seheli* (currently *Moolgarda seheli*), the type species of *Valamugil*, clusters with *C. crenilabis* (the type species of *Crenimugil*) into a single, well supported subclade. The subclade that includes *M. cunnesius*, *M. engeli* and *M. perusii* should now be assigned to Lüther's [42] *Osteomugil*. It is remarkable that Senou's [10] cladistic treatment, based on morphological characters, yielded the same result regarding the *Crenimugil*/*Moolgarda*/*Valamugil* group (Fig. 3) as the present molecular phylogeny (Fig. 2C). Senou [10] however fell short of proposing that *M. seheli* and *V. buchani* be placed under *Crenimugil*, and that *M. cunnesius*, *M. engeli* and *M. perusii* be placed under *Osteomugil*. *Valamugil robustus* was the most externally branching species relative to the other species in our *Osteomugil* subclade. Therefore, although here we placed *V. robustus*, *M. cunnesius*, *M. engeli* and *M. perusii* under a single genus, it may be argued that *V. robustus* be assigned a different genus name because of the large nucleotide

distance that separates it from the other species in the sub-clade. The unique position of the first dorsal fin in *V. robustus* relative to all the other *Valamugil* spp. and *Moolgarda* spp. [11] would provide morphological support for this distinction. Nevertheless, we adopted a conservative approach and we leave this taxonomic problem to future research. The genus *Osteomugil* under its present, revised definition has a wide Indo-Pacific distribution, from South Africa to French Polynesia [11].

3.20. *Xenomugil*

The *Xenomugil thoburni* partial haplotypes were found to be embedded within the *Mugil curema* haplogroup (Fig. 2C). Therefore, there is no phylogenetic rationale to recognizing the genus *Xenomugil* as valid. The placement of *X. thoburni* haplotypes within the *Mugil* spp. subclade implies that *Xenomugil* is a synonym of *Mugil*. Further research is needed to clarify the systematics of the *M. curema* species complex and, in particular, whether *X. thoburni* is a distinct, biological species.

4. Conclusion

All phylogenetic hypotheses based on morphology and morpho-anatomy proposed within the last few decades for Mugilidae (review in [1]) were in contradiction with one another and the molecular phylogenetic results [1] supported no one. Here, we proposed a new classification that is consistent with the molecular phylogeny of [1], resurrecting genus names previously fallen into oblivion and eventually pointing out the need for new genus names in cases where no name is available [51]. The revised classification of the Mugilidae family proposed here recognizes 25 genera, including 15 genera currently considered as valid (*Agonostomus*, *Aldrichetta*, *Cestraeus*, *Chaenomugil*, *Chelon*, *Crenimugil*, *Ellochelon*, *Jotur*, *Mugil*, *Myxus*, *Neomyxus*, *Oedalechilus*, *Rhinomugil*, *Sicamugil* and *Trachystoma*) and 6 resurrected genera (*Gracilimugil*, *Minimugil*, *Osteomugil*, *Planiliza*, *Plicomugil* and *Squalomugil*). The mitochondrial phylogeny also singled out three isolated lineages (currently *L. falcipinnis*, *Myxus capensis*, and *L. grandisquamis*) for which no genus name is yet available. We here propose the following new genus names: *Neochelon* gen. nov. (type species: *Mugil falcipinnis* Valenciennes 1836); *Parachelon* gen. nov. (type species: *M. grandisquamis* Valenciennes 1836); and *Pseudomyxus* gen. nov. (type species: *M. capensis* Valenciennes 1836). Further genetic evidence is required to confirm or infirm the validity of genus *Paracrenimugil* proposed by Senou [10] for *C. heterocheilos*, as no genetic data are yet available for this species. Genus names *Liza*, *Moolgarda*, *Paramugil*, *Valamugil* and *Xenomugil* were shown to be invalid and they should now be abandoned.

More research is needed to address taxonomic issues at the infra-generic level. For instance, *Agonostomus monticola* and several species with large distribution ranges (including *Moolgarda seheli*, *Mugil cephalus* and *M. curema*) consisted of separate lineages whose geographic distribution suggests they are cryptic species (Figs. 1 and 2). Nuclear-DNA markers are powerful to detect reproductive

isolation among cryptic species in sympatry. Nuclear genotyping has already led to identifying three biological species within *M. cephalus* from Taiwan [55] and two biological species within *M. curema* from the central western Atlantic [1]. Given the general helplessness of morphology and morpho-anatomy to reconstruct a consistent phylogeny of Mugilidae, a central role should now be assigned to molecular phylogenetics and population genetics in the taxonomy of species in this family.

5. Taxonomic description of three new mugilid genera

5.1. *Neochelon*, new genus

The new genus name *Neochelon* is here proposed for *Mugil falcipinnis* Valenciennes 1836 [18], here designated as its type species. The nucleotide sequences examined were those of the *cytb* gene (GENBANK accession No. JQ060212), the *COI* gene (GENBANK JQ060469), and the *16S* gene (GENBANK JQ060716) of voucher specimen no. MNHN 2009-0730 (from Toubacouta, Saloum estuary, Senegal), and the homologous sequences of specimens collected in St Louis, Senegal (GENBANK JQ060213, JQ060470, and JQ060717; JQ060214, JQ060471, and JQ060718) and at the fish market of Lome, Togo (GENBANK JQ060215, JQ060472, and JQ060719) (Table 1 of [1]). The new genus is unique by the placement of its mitochondrial haplotypes on the phylogenetic tree of Mugilidae (Fig. 1), alone forming one of the seven major clades that stem from the common ancestor to all current mugilid species. The name of the genus is derived from *Chelon*, preceded by greek prefix “neo-” meaning “new”. Distribution: West Africa, from Saint-Louis in northern Senegal to Congo [11].

5.2. *Parachelon*, new genus

The new genus name *Parachelon* is here proposed for *Mugil grandisquamis* Valenciennes 1836 [18], here designated as its type species. The nucleotide sequences examined were those of the *cytb* gene (GENBANK accession nos. JQ060218 and JQ060219), the *COI* gene (GENBANK JQ060475 and JQ060476), and the *16S* gene (GENBANK JQ060722 and JQ060723) of voucher specimens nos. MNHN 2009-731 and SAIAB-83182 (both from Saloum

estuary, Senegal), and the homologous sequences of additional specimens collected in the Saloum estuary, Senegal (GENBANK JQ060216, JQ060473, and JQ060720) and at the fish market in Bissau, Guinea Bissau (GENBANK JQ060217, JQ060474, and JQ060721). This new genus is unique by the placement of its mitochondrial haplotypes on the phylogenetic tree of Mugilidae (Fig. 1), where it forms a subclade sister to *Chelon*, *Oedalechilus*, and *Planiliza* within the clade that also comprises *Pseudomyxus* gen. nov. The name of the genus is derived from *Chelon*, preceded by greek prefix “para-” meaning “beside”. Distribution: West Africa, from Senegal to Nigeria [11].

5.3. *Pseudomyxus*, new genus

The new genus name *Pseudomyxus* is here proposed for *Mugil capensis* Valenciennes 1836 [18], here designated as its type species. The nucleotide sequences examined were those of the *cytb* gene (GENBANK JQ060366), the *COI* gene (GENBANK JQ060615) and the *16S* gene (GENBANK JQ060867) of a specimen collected in the East Kleinemonde estuary, South Africa (sampling details in Table 1 of [1]). The new genus is unique by the placement of its mitochondrial haplotypes on the phylogenetic tree of Mugilidae (Fig. 1): *Pseudomyxus* gen. nov., together with *Chelon*, *Oedalechilus*, *Parachelon* gen. nov. and *Planiliza*, forms one of the seven major clades of the Mugilidae family. *Pseudomyxus* gen. nov. represents the most external lineage within this clade (Fig. 1). The name of the genus is derived from *Myxus*, preceded by greek prefix “pseudo-” meaning “false”. Distribution: South Africa [11].

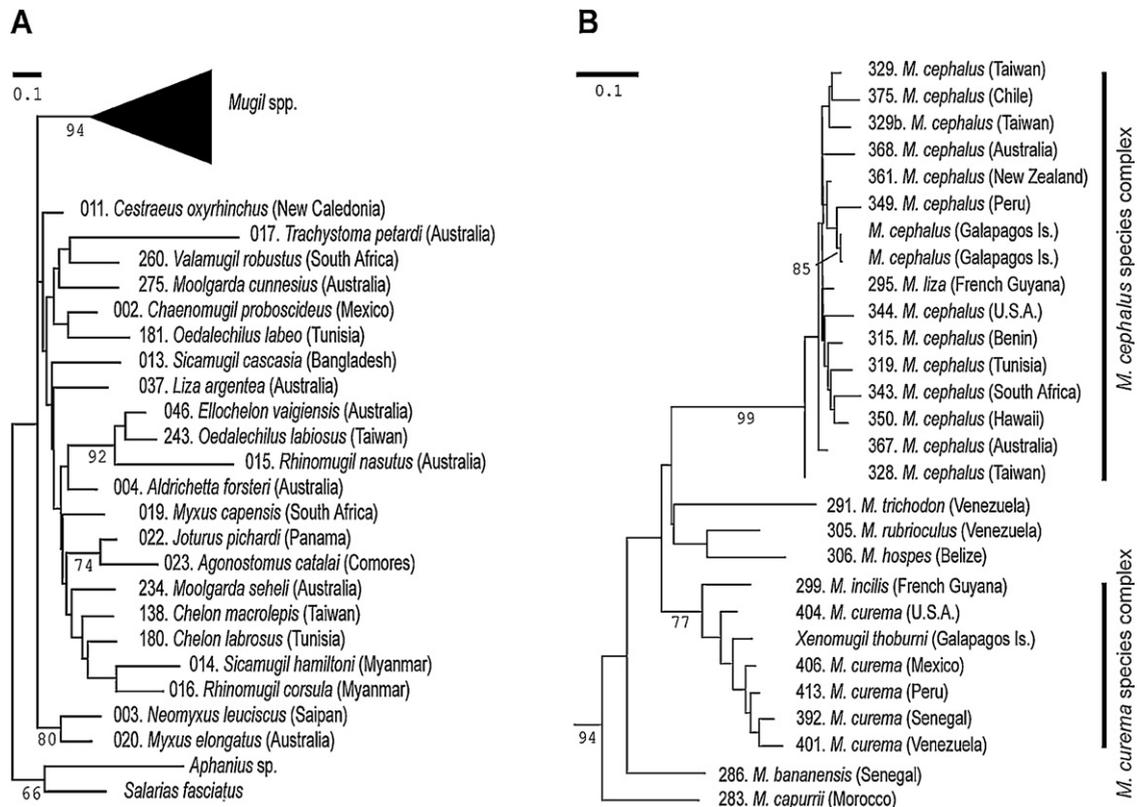
Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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Appendix A



Molecular phylogenetic analysis of Mugilidae partial sequences (300 bp) of the *cytb* gene, inferred by using the Maximum Likelihood method from Tamura and Nei's [48] model as implemented in MEGA 5 [49]. A. Entire tree with the highest log-likelihood [$\ln(L) = -5162.2$]. Sequences for outgroups *Arcos* sp. (Gobirosidae) and *Salarias fasciatus* (Blenniidae) [50] are from GenBank (<http://www.ncbi.nlm.nih.gov/>; accession nos. AP004452 and AP004451, respectively). B. Detail of the *Mugil* subtree; sequences of *Xenomugil thoburni* and two *M. cephalus* from the Galapagos Islands were kindly provided by S. Livi (pers. comm.). The percentage of pseudotrees generated by bootstrap resampling (500 runs), in which the associated individuals clustered together is shown next to the branches (bootstrap scores below 70% not shown). Branch length is proportional to the number of substitutions per site. Specimen numbers refer to Table 1 of [1].

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