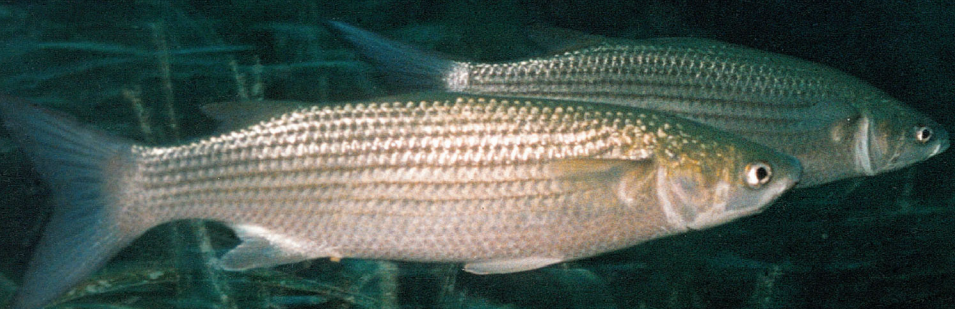
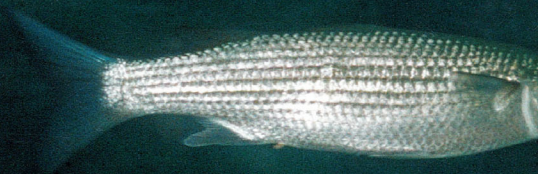


Biology, Ecology and Culture of Grey Mullet (Mugilidae)

Editors

Donatella Crosetti

Stephen Blaber



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Grey Mullet (*Mugilidae*)**

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- Grey mullets from aquaculture. Photo by I. Chiu Liao.

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Preface

The Mugilidae, commonly known as grey mullets, are one of the most ubiquitous teleost families in coastal waters of the world. They occur in most temperate, sub-tropical and tropical waters in both hemispheres. As a family they have an extraordinary adaptability, which has resulted in species that are found mainly in the clear and pristine waters of coral reefs to those that prefer highly turbid estuarine and fresh waters. Some species can even survive in some of the most polluted waters in the world, e.g., in the harbour at Viskhapatnam in India (Blaber 2000). Wherever grey mullet occur they often dominate the fish fauna and due to their primarily detritivorous feeding occupy a unique position in the food web. In some areas their species diversity may be very high, e.g., in the St. Lucia coastal lake system in South-East Africa at least 10 species are sympatric (Blaber 1976). Not surprisingly these fish are economically important in most regions, particularly the worldwide species *Mugil cephalus*, which forms the basis of significant commercial fisheries in developed parts of the world such as Australia and the U.S.A., as well as vital artisanal and subsistence fisheries in developing countries. Mulletts are also cultured in many regions of the world, both in extensive systems, such as the more or less confined coastal lagoon areas in the Mediterranean region, and in semi-intensive and intensive systems, often in polyculture with other species, though culture is still based on the collection of wild fry, as no induced spawning is practiced at a commercial level. Egypt is by far the greatest producer of cultured grey mullets, with 84% of the world mullet aquaculture production (138,143 tonnes in 2013, FAO 2015).

Mugilidae taxonomy and nomenclature have been revised several times, and a critical revision is ongoing at present, with the new information provided by molecular tools which certainly represent a great challenge to the traditional morphologically based taxonomy (see Chapters 1 and 2). Indeed Mugilidae are very conservative in morphological traits, a characteristic of the family which may have led in the past to misidentifications and erroneous synonymies among taxa, especially from specimens from regions of the world that are far apart. Many taxonomic issues are still being debated and will probably lead in the near future to a total upset of the family taxonomy and nomenclature. For practical reasons, the Mugilidae nomenclature used in the Eschmeyer 'Catalog of fishes' (2015) was adopted for all chapters of this book, and possible eventual synonyms or new species names cited by other authors are reported in brackets.

The last comprehensive review of the Mugilidae was published more than 30 years ago in 1981 (Oren 1981). Although this book concentrated mainly on aquaculture, it also provided syntheses of much of the biological and ecological knowledge available at the time. A subsequent book by Hussenot and Gauthier (2005) published in French provided valuable information on the European grey mullets. An excellent review of the biology, genetics, ecology and fisheries of *M. cephalus* was recently published (Whitfield et al. 2012). This review was one of the outputs of the EU funded project MUGIL (see Chapter 21) and deals with all the most important issues of *M. cephalus* biology and ecology. It is restricted however, to this one species. Recent advances in knowledge, including great leaps forward in ecological and biological information from many tropical developing countries, more intensive taxonomic investigations and biogeographical studies coupled with advances in genetic techniques, and major advances in applied aquaculture, indicate that a new review of what is known about the Mugilidae is overdue.

The present volume hopes to go some way towards filling this gap. It is divided into two sections, the first dealing with biology, ecology and systematics, and the second with culture and fisheries.

The first two chapters are concerned with taxonomy and systematics. Chapter 1 by González-Castro and Ghasemzadeh reviews and discusses the present status of mugilid taxonomy around the world, and shows how both the traditional and new techniques and tools can be used to identify the many species in this family. Unfortunately, the close similarities in the morphology and anatomy of most grey mullet species have made difficult the tasks of inferring phylogenetic relationships and evolution, as well as the identification of species and genera. Hence there has been little consensus on the systematics of the family. In Chapter 2, Durand describes how genetic polymorphisms, which constitute a valid and powerful alternative to morphology, can be used to test the prevailing phylogenetic assumptions based upon morphological traits. He demonstrates the implications of recent molecular phylogeny for the taxonomy of the Mugilidae, concluding that there is more and more molecular evidence that the species diversity of the Mugilidae is greatly underestimated.

The next five chapters provide much new information about the biogeography and distribution of Mugilidae in different regions of the world. In Chapter 3, Barletta and Dantas document the situation in the Americas; in Chapter 4, the biogeography of Mugilidae in India, South-East and East Asia is described by Shen and Durand and the same is done for Australia and Oceania by Ghasemzadeh in Chapter 5; in Chapter 6, Durand and Whitfield describe the biogeography and distribution of African Mugilidae; the biogeography of Mugilidae in the Mediterranean, Europe and the North-East Atlantic is explained by Turan in Chapter 7.

Biological and ecological information is provided in the next five chapters. The musculoskeletal anatomy of the flathead grey mullet *Mugil cephalus* is described in great detail in Chapter 8 by Ghasemzadeh and this chapter contains several line drawings of the most important skeletal bones. Chapter 8 thus provides a sound basis for future comparisons with the osteology of other mullet species. The variously described mud-eating, iliophagy, detritus feeding, deposit feeding and interface feeding habits of grey mullet are detailed by Cardona in Chapter 9. Age and growth are described by Ibáñez in Chapter 10, reproduction by González-Castro and Minos in Chapter 11, the biology of fry and juveniles by Koutrakis in Chapter 12, and their remarkable adaptations to salinity and their osmoregulation are discussed by Nordlie in Chapter 13. The very significant ecological role of grey mullet in coastal waters and estuaries around the world is described by Whitfield in Chapter 14. Rossi, Crosetti and Livi have provided a very eloquent overview in Chapter 15 of research on the genetics of Mugilidae, with particular reference to *Mugil cephalus*.

The second part of the book begins with Chapter 16 by Crosetti on the current status of mullet capture fisheries and their aquaculture. This is followed by Chapter 17 by Prosser on capture methods and commercial fisheries, and then Chapter 18 by Leber et al. on culture-based stock enhancement, with particular reference to Hawaii. The next two Chapters 19 and 20 provide detailed case studies of the culture industries in Taiwan and Egypt by Liao, Chao and Tseng and Sadek respectively. The book concludes with a chapter about the MUGIL project, which involved scientists from eight countries collaborating to document what was known in 2009 about all aspects of *Mugil cephalus*.

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The editors would like to thank most sincerely all the authors for their contributions. The hard work that has gone into the research and reviewing of the literature is evident in each of the chapters. It has been a truly collaborative effort with scientists coming together from around the world to analyse what is known about this important worldwide family of fishes. Donatella Crosetti is thankful to Giovanna Marino, the head of the Aquaculture Department in ISPRA (Italian Institute for Environmental Protection and Research), who believed in this project and included it in the activities of the Aquaculture Department, and would like to acknowledge ISPRA and FAO (Food and Agriculture Organization of the United Nations) Libraries for their support in collecting bibliographic references. Stephen Blaber is grateful to CSIRO (Commonwealth Scientific and Industrial Research Organisation) Oceans and Atmosphere in Brisbane, Australia, for research facilities. We are also very grateful to all at CRC Press for their help and forbearance in seeing this book to fruition.

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CHAPTER 1

Morphology and Morphometry Based Taxonomy of Mugilidae

Mariano González-Castro^{1,*} and Javad Ghasemzadeh²

Introduction

The Critical State of the Taxonomy of Mugilidae

Members of the family Mugilidae, generally known as mullets, are coastal marine fishes with a worldwide distribution including all temperate, subtropical and tropical seas. They not only inhabit offshore and coastal waters, but also depending on the species, spend part or even their whole life cycle in coastal lagoons, lakes and/or rivers. A considerable period of time has passed since the last book was published on Mugilidae (Oren 1981). Many important and critical changes related to the taxonomy and systematics of this family have taken place since this last publication. We may perhaps be in the ‘middle of a revolution’, with regard to the phylogeny and taxonomy of mullets. New and more efficient methodologies have developed in the past few decades, which improve the accurate discrimination of taxa; for example the sequencing of mitochondrial and/or nuclear genes (molecular taxonomy) and the geometric morphometrics (a relatively novel discipline which is based on the use of anatomical landmarks in order to evaluate differences in the shape of organisms). As could be expected, as a consequence of the application of these new techniques, new results have been obtained on Mugilidae, such as the appearance of cryptic species, but also conflicts have arisen at the generic and even subfamily levels. Table 1.1 summarizes the nominal genera of Mugilidae, in chronological order of appearance, with their status according to different authors.

Much more work has to be done in order to clarify and consolidate the taxonomy and systematics of Mugilidae. Hence, the aim of this chapter is to review and discuss the present status of mugilid taxonomy around the world, and also to show both the traditional and new tools that can be employed to identify/discriminate these fishes.

What are Mulletts?

Fishes of the family Mugilidae belong to Actinopterygii, which is the class that groups the highest number of species, has the most recent expansion and manifests more notable evolutionary lines toward both slender

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<i>Liza</i>	Jordan and Swain 1884	<i>Mugil capito</i> Cuvier 1829	<i>Chelon</i>	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>	<i>Liza</i>
<i>Trachystoma</i>	Ogilby 1888	<i>Trachystoma multidentis</i> Ogilby 1888	<i>Trachystoma</i>	<i>Chelon</i>	<i>Myxus</i>	<i>Trachystoma</i>	<i>Trachystoma</i>	<i>Trachystoma</i>
<i>Neomugil</i>	Vaillant 1894	<i>Neomugil digueti</i> Vaillant 1894	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Agonostomus</i>	<i>Dajaus</i>	<i>Agonostomus</i>
<i>Oedalechilus</i>	Fowler 1903	<i>Mugil labeo</i> Cuvier 1829	<i>Chelon</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>
<i>Squalomugil</i>	Ogilby 1908	<i>Mugil nasutus</i> de Vis 1883	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Rhinomugil</i>	<i>Squalomugil</i>
<i>Xenorhynchichthys</i>	Regan 1908	<i>Joturus stipes</i> Jordan and Gilbert 1882	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>	<i>Joturus</i>
<i>Ellochelone</i>	Whitley 1930	<i>Mugil vaigiensis</i> Quoy and Gaimard 1825	<i>Chelon</i>	<i>Ellochelone</i>	<i>Liza</i>	<i>Ellochelone</i>	<i>Ellochelone</i>	<i>Ellochelone</i>
<i>Protomugil</i>	Popov 1930	<i>Mugil saliens</i> Risso 1810	-	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>	<i>Liza</i>
<i>Sicamugil</i>	Fowler 1939	<i>Mugil hamiltoni</i> Day 1869	<i>Trachystoma</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>
<i>Gracilmugil</i>	Whitley 1941	<i>Mugil ramsayi</i> Macleay 1883	<i>Trachystoma</i>	<i>Chelon</i>	<i>Liza</i>	<i>Gracilmugil</i>	<i>Gracilmugil</i>	<i>Liza</i>
<i>Moolgarda</i>	Whitley 1945	<i>Moolgarda pura</i> Whitley 1945	-	<i>Moolgarda</i>	<i>Valamugil</i>	<i>Valamugil</i>	-	<i>Moolgarda</i>
<i>Planiliza</i>	Whitley 1945	<i>Moolgarda</i> (Planiliza) <i>ordensis</i> Whitley 1945	-	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>	<i>Liza</i>
<i>Aldrichetta</i>	Whitley 1945	<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	<i>Mugil thoburni</i> Jordan and Starks 1896	<i>Xenomugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Mugil</i>	<i>Xenomugil</i>
<i>Crenimugil</i>	Schultz 1946	<i>Mugil crenilabis</i> Forskal 1775	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>
<i>Oxymugil</i>	Whitley 1948	<i>Mugil acutus</i> Valenciennes 1836	-	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>	<i>Liza</i>
<i>Pteromugil</i>	Smith 1948	<i>Mugil diadema</i> Gilchrist and Thompson 1911	-	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>	<i>Liza</i>
<i>Sriializa</i>	Smith 1948	<i>Mugil canaliculatus</i> Smith 1935	<i>Chelon</i>	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Chelon</i>	<i>Liza</i>
<i>Valamugil</i>	Smith 1948	<i>Mugil seheli</i> Forsska ^a 11775	-	<i>Moolgarda</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Crenimugil</i>	<i>Valamugil</i>

Table 1.1. contd....

Table 1.1. contd.

Genus	Author and date	Type species	Genus assigned by author (date)					
			Schultz (1946)	Senou (1988)	Thomson (1997)	Ghasemzadeh (1998)	Durand et al. (2012b)	Eschmeyer and Fong (2015)
<i>Plicomugil</i>	Schultz 1953	<i>Mugil labiosus</i> Valenciennes 1836	-	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Oedalechilus</i>	<i>Plicomugil</i>	
<i>Osteomugil</i>	Luther 1977	<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	<i>Mugil cascasi</i> Hamilton 1822	-	<i>Minimugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>	<i>Sicamugil</i>
<i>Paracrenimugil</i>	Senou 1988	<i>Mugil heterochelios</i> Bleeker 1855	-	<i>Paracrenimugil</i>	<i>Crenimugil</i>	<i>Crenimugil</i>	ND	<i>Crenimugil</i>
<i>Pseudoliza</i>	Senou 1988	<i>Mugil parmatus</i> Cantator 1849	-	<i>Pseudoliza</i>	<i>Liza</i>	<i>Liza</i>	<i>Planiliza</i>	<i>Paramugil</i>
<i>Paramugil</i>	Ghasemzadeh 1998	<i>Mugil parmatus</i> Cantator 1849	-	<i>Pseudoliza</i>	<i>Valamugil</i>	<i>Valamugil</i>	<i>Paramugil</i>	<i>Paramugil</i>
<i>Neochelon</i>	Durand et al. 2012b	<i>Mugil falcipinnis</i> Valenciennes 1836	-	<i>Chelon</i>	<i>Liza</i>	-	<i>Neochelon</i>	<i>Neochelon</i>
<i>Parachelon</i>	Durand et al. 2012b	<i>Mugil grandisquamis</i> Valenciennes 1836	-	<i>Chelon</i>	<i>Liza</i>	<i>Liza</i>	<i>Parachelon</i>	<i>Parachelon</i>
<i>Pseudomyxus</i>	Durand et al. 2012b	<i>Mugil capensis</i> Valenciennes 1836	-	<i>Chelon</i>	<i>Myxus</i>	<i>Myxus</i>	<i>Pseudomyxus</i>	<i>Pseudomyxus</i>

and faster forms (Nelson 2006, Cousseau 2010). There has been, and there is still, much disagreement concerning the evolutionary relationships of the order Mugiliformes, represented by a single family. While the monophyly of this family has never been challenged, phylogenetic placement of this enigmatic assemblage has been a long standing problem of systematic ichthyology (Stiassny 1993). Berg (1940) placed the Atherinidae, Mugilidae and Sphyraenidae in the order Mugiliformes, but at the Subperciformes level. Subsequently, Greenwood et al. (1966) and Nelson (1984) reviewed the subordinal status of these three families, and placed them in the order Perciformes. Later Nelson (1994, 2006) placed them in the order Mugiliformes.

The species of Mugilidae are characterized not only by both a remarkably uniform external morphology, but also a scarcely less so internal anatomy. This can be demonstrated by a comparison of the attributes commonly employed to identify mullets, as the number of scales, fin spines and fin rays, and measurements of body proportions (González-Castro 2007). They are medium to large-sized fishes, reaching a maximum size of 120 cm standard length, but commonly to about 30 cm standard length; subcylindrical body; head often broad and flattened dorsally (rounded in *Agonostomus* and *Joturus*) (Harrison and Senou 1999).

Mullets have two widely separated dorsal fins, the first of four spines and the second one usually with an unbranched ray (often called a spine) and six–10 branched rays. The pelvic fins are sub-abdominal, with a spine and five branched rays. The anal fin has two–three spines and eight–12 branched rays. The lateral line is absent, and adult mullets usually have ctenoid scales. The mouth is of moderate size, with small (labial) or missing teeth. The gill arches are usually long. They have a muscular stomach and an extremely long intestine. They have 24–26 vertebrae (Nelson 2006).

Traditionally, the features of diagnostic value for Mugilidae included: the structure of scales, the relative position of the nostrils, the number and shape of the gill rakers, the form of the preorbital, the relative lengths of the paired fins and of their axillary scales and the position of origin of the various fins, the presence or absence of an adipose eyelid and the degree of intrusion over the eye, as well as the number of pyloric caeca and the relative length of the intestine (Thomson 1997). More recently the body shape, and also the scales have been analyzed by means of geometric morphometrics. They proved to be useful as a discriminating tool at the specific and population levels (Corti and Crosetti 1996, Heras et al. 2006, Ibáñez et al. 2007, González-Castro et al. 2012). Mullet also possess a characteristic oral and branchial filter-feeding-mechanism involving gill rakers and a specialized pharyngobranchial organ comprising a large, denticulate pharyngeal pad and pharyngeal sulcus on each side of the pharyngobranchial chamber (Harrison 2002).

A Historical Overview of the Diagnostic Osteo-Morphological Features used in the Main Reviews of the Genera of Mulletts

Schultz (1946) made a comprehensive revision of the genera of Mugilidae. He paid attention to the taxonomic importance of mouth parts and other qualitative characters such as the position (inferior or terminal) of the mouth, the relative thickness of the lips, the degree of lips' coverage by papillae and crenulations, the nature of the upper attachment of the maxilla, the curvature and degree of exposure of the posterior angle of the maxilla, the morphology and distribution of teeth, and the presence or absence of the symphysial knob. On the basis of these characters he recognized a total of 13 genera (including three new genera which were created/described by him) namely: *Cestraeus* Valenciennes 1836; *Joturus* Poey 1860; *Rhinomugil* Gill 1863; *Agonostomus* Bennett 1831; *Chaenomugil* Gill 1863; *Neomyxus* Steindachner 1878; *Xenomugil* Schultz 1946; *Crenimugil* Schultz 1946; *Mugil* Linnaeus 1758; *Myxus* Günther 1861; *Chelon* Artdi 1793; *Trachystoma* Ogilby 1888 and *Heteromugil* Schultz 1946. Figure 1.1 shows the possible relationships of the genera of Mugilidae according to Schultz (1946).

Smith (1948) conducted a generic revision of the South African mullets, and applied the characters used by Schultz. He confirmed the taxonomic value of the mouthparts, but noted that Schultz did not examine world-wide representatives. Smith (1948) added five more genera to those described by Schultz (1946). Again Schultz (1953) reviewed his own, and Smith's work, and after making corrections and additions, accepted 14 genera as valid.

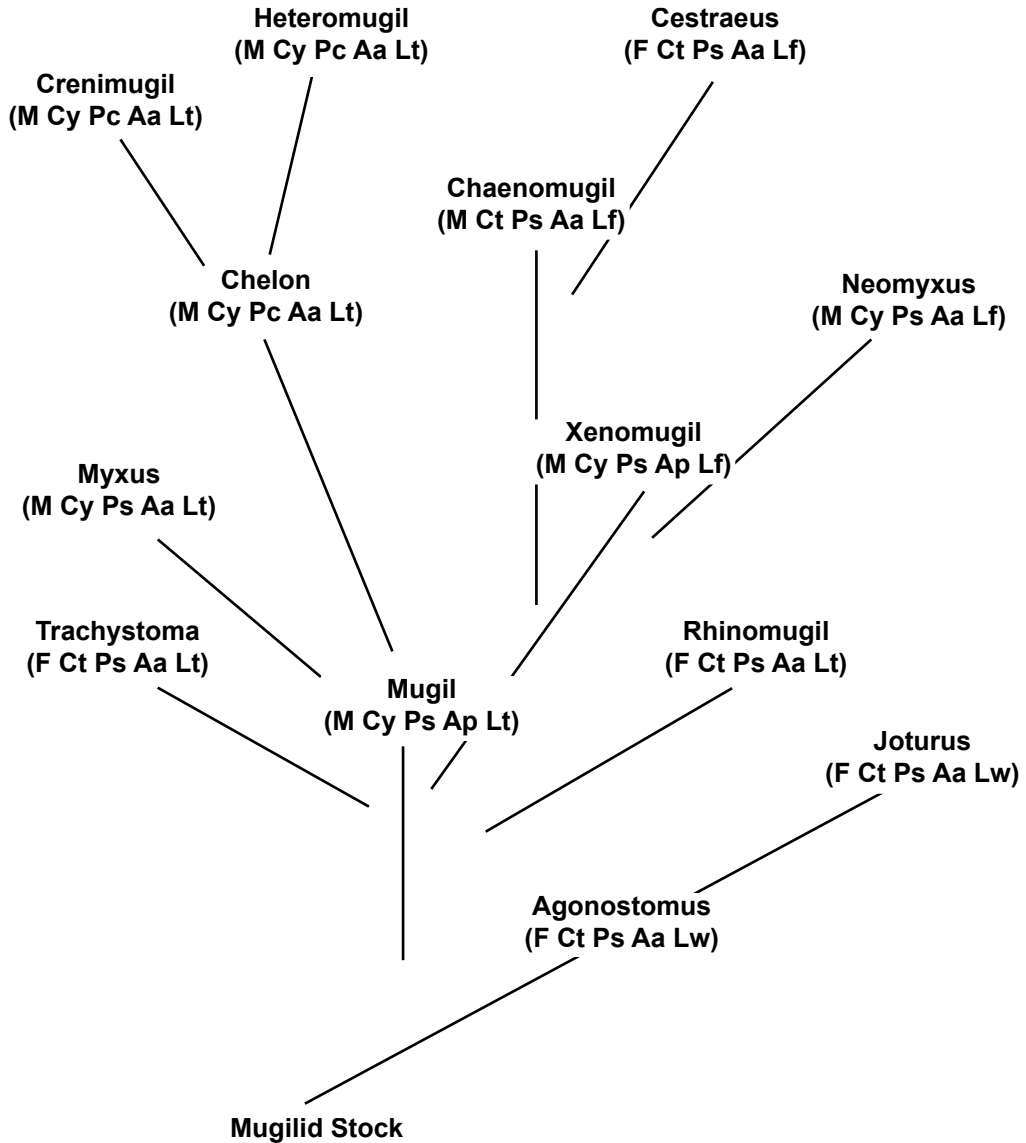


Figure 1.1. Diagram of the possible relationships of genera of the Mugilidae. Letters in the parentheses under each genus indicate some of the characters used in forming an opinion on the general evolutionary trends (Aa.-Adipose eyelid absent; Ap.-Adipose eyelid present; Ct.-Ctenoid scales; Cy.-Cycloid scales; F.-Freshwater habitat; Lf.-Lower lip folded downward; Lt.-Lower lip with thin edge projecting forward; Lw.-Lower lip thickish; M.-Marine habitat and entering brackish waters; Pc.-Front edge of preorbital straight and the maxillary and premaxillary extending in the same general line as front edge of preorbital; Ps.-Front edge of preorbital concave or deeply notched, the maxillary and premaxillary bent at an abrupt angle posteriorly, and exposed below preorbital) (from Schultz 1946).

Ingham's (1952, unpublished thesis) comprehensive revision of the biology and taxonomy of mullets (based principally on examination of the material in the British Museum of Natural History) recognized 67 species in 13 genera, and indicated that another 11 species were possibly valid.

Thomson (1954a) conducted a revision of the mullets of Australian waters and adjacent seas, based on characters of mouth parts, dentition, digestive system, morphometric and meristics. He listed 38 nominal genera (excluding fossils) world-wide, of which 13 genera were recognized as valid, and described

17 species belonging to nine genera in Australia and the South Pacific region. Thomson (1981) considered 64 species in 14 genera (of 282 nominal species) as valid, and presented a detailed description of distinctive characters and diagnostic features useful for recognition of mullet species.

Senou (1988, unpubl. thesis) reviewed the phylogenetic relationships of mullets, using osteological and morphological characters. He recognised 44 species (17 genera) in two subfamilies, Agonostominae (with three genera) and Mugilinae (14 genera).

Thomson (1997) undertook a world-wide revision of the family Mugilidae. He included some new features of diagnostic value such as the structure of the scales, the relative position of the nostrils, the number and form of the gill rakers, the shape of the preorbital, the relative length of the paired fins and of their axillary scales, the position of the origin of the various fins, the presence or absence of the adipose eyelid and the degree of its intrusion over the eye, as well as the number of pyloric caeca and the relative length of the intestine. This author recognized as valid 14 of 40 described genera, and 62 of 280 nominal species. He also introduced a new species (*Liza mandapamensis*), and classified 18 species as *inquerenda*.

Thomson (1997) accepted the division of the family Mugilidae by Jordan and Evermann (1896) into two subfamilies of Agonostominae and Mugilinae, mainly based on the character of presence or absence of sessile teeth on the jaws, the shape of the lower jaw and the degree of complexity of the stomach. The genera *Joturus* Poey 1860, *Agonostomus* Bennett 1831, *Cestraeus* Valenciennes 1836 and *Aldrichetta* Whitley 1945 belonged to the subfamily Agonostominae while the subfamily Mugilinae included the genera *Rhinomugil* Gill 1863, *Sicamugil* Fowler 1939, *Chaenomugil* Gill 1863, *Oedalechilus* Fowler 1903, *Crenimugil* Schultz 1946, *Chelon* Artedi 1793, *Mugil* Linnaeus 1758, *Myxus* Günther 1861b, *Valamugil* Smith 1948 and *Liza* Jordan and Swain 1884.

Ghasemzadeh (1998) reviewed the systematics, phylogeny and distribution of Indo-Pacific and Australian mullets, using morphological and osteological data. He recognized 18 of the 40 world-wide described genera as valid and described a new genus *Paramugil* (Ghasemzadeh et al. 2004). He also described 27 species belonging to 14 genera in Indo-Pacific and Australian waters.

Eschmeyer and Fong (2015) and Eschmeyer (2015) performed the last revision of the systematics of Mugilidae. They recognized 20 genera and 71 species. The species names of the present book will refer to this catalogue. The following genera are recognized as valid: *Cestraeus* Valenciennes 1836, *Agonostomus* Bennett 1832, *Aldrichetta* Whitley 1945, *Mugil* Linnaeus 1758, *Chaenomugil* Gill 1863, *Chelon* Artedi 1793, *Crenimugil* Schultz 1946, *Ellochelon* Whitley 1930, *Liza* Jordan and Swain 1884, *Joturus* Poey 1860, *Moolgarda* Whitley 1945, *Myxus* Günther 1861, *Neochelon* Durand et al. 2012b, *Neomyxus* Steindachner 1878, *Oedalechilus* Fowler 1903, *Parachelon* Durand et al. 2012b, *Pseudomyxus* Durand et al. 2012b, *Rhinomugil* Gill 1863, *Sicamugil* Fowler, 1939, *Trachystoma* Ogilby 1888.

Morphological and Meristic Diagnostic Characters Traditionally Employed for Taxonomic Determination of Mugilidae

The identification and taxonomy of mullets has relied on external morphology, meristics, morphometrics and the structure of some internal organs. The remarkably uniform external morphology of mullets has resulted in continuous confusion in their identification and classification. Further taxonomic confusion has been due to the wide range of variability in characters examined, and slight diagnostic differences between species (Ghasemzadeh 1998).

Characters which have been used by different authors include dentition (Ebeling 1957, 1961, Thomson 1975, Farrugio 1977), scales (Cockerell 1913, Jacot 1920, Pillay 1951, Thomson 1981, Chervinski 1984, Liu and Shen 1991, Ibáñez et al. 2011), number of pyloric caeca (Perlmutter et al. 1957, Hotta and Tung 1966, Luther 1977), the alimentary tract (Thomson 1966), intestinal convolution (Hotta 1955), osteology (Ishiyama 1951, Hotta and Tung 1966, Sunny 1971, Kobelkowsky and Resendez 1972, Luther 1977, Senou 1988, Ghasemzadeh 1998), otoliths (Morovic 1953), morphology of the cephalic lateral line canals (Song 1981), pharyngobranchial organ (Harrison and Howes 1991), and dentition, pigmentation and melanophore patterns in identification of fry and juveniles (van der Elst and Wallace 1976, Cambrony 1984, Reay and Cornell 1988, Serventi et al. 1996, Minos et al. 2002). Following a brief description,

characters and features of diagnostic value which are commonly used in identification and taxonomy of mullets are given.

Adipose Eyelid

The adipose membrane is not a third eyelid, but a fatty deposition on the head around the eyes which can be present or absent, depending on the genera. This tissue is transparent in life, and becomes opaque on death. As used in most keys and descriptions, the extent of the development of the adipose eyelid refers only to mature specimens (Thomson 1954a). This tissue is not developed in newly hatched fish, and does not become apparent until a length of 4 or 5 cm, after which the area of the eye covered may continually increase during life (e.g., *Mugil cephalus*) or remain relatively insignificant as in some species of the genus *Liza*. The terminology for recording the extent of the development of the adipose eyelid is not very exact, and most authors use the terminology which was suggested by Thomson (1954a). The term 'absent' indicates that no trace of an adipose eyelid could be found. The terms 'obsolescent' or 'rudimentary' refer to any stage between a rim around the eye to a lid covering up to a third of the iris; and 'present' indicates the development beyond a mere rim, so as to cover a measurable portion of the eye. Thus, this character is commonly employed to differentiate between genera. Thomson (1981) points out that the occurrence of varying width within different genera suggests that the genera diverged after the development of the adipose tissue in the Mugilinae subfamily, with subsequent independent trends to obsolescence of this characteristic.

Pyloric Caeca

The number of pyloric caeca varies among mullet species, and can be of some taxonomic importance, especially among different genera. The primitive number of two pyloric caeca is found throughout the subfamily Agonostominae and in *Trachystoma*, *Gracilimugil*, *Neomyxus*, *Myxus* (except *Myxus capensis*), *Mugil*, *Sicamugil* and *Chaenomugil* of Mugilinae (Thomson 1997, Ghasemzadeh 1998). In other genera the number of pyloric caeca varies between three and 48 (usually, between five and 10). However, its counting assumes the dissection of the specimen, so this meristic characteristic is not useful in eviscerated (i.e., museum) specimens. Also, it requires extra time in order to perform the dissection, which makes this feature unsuitable for quick taxonomic identification on the field.

Normally, the number of pyloric caeca varies within a certain range in specimens of the same species, but it is usual to find well differentiated species of the same genus sharing the same number of pyloric caeca.

Teeth

The teeth are important anatomical elements which can be employed as diagnostic features in taxonomy of mullets. In the plesiomorphic Agonostominae the jaw teeth are of proximal or sessile type (Jordan and Evermann 1896, Fink 1981, Thomson 1997, Ghasemzadeh 1998), and borne directly on the premaxilla and dentary bones. In Mugilinae, the jaw teeth are minute and labial, and are borne on the distal end of flexible and closely packed fibrous strands, which are proximally joined to the premaxilla and dentary, and supported by labial tissue (Thomson 1997, Ghasemzadeh 1998). In many species of mullet, only a single row of teeth is developed which is referred to as primary teeth (Ebeling 1957), but in others there may be several inner rows (termed secondary teeth). In some species the form of the primary and secondary teeth are different, and since distal-type teeth are loosely attached to the underlying bone, they are presumably often lost and replaced (Ebeling 1957). However, in mullets there is a tendency for teeth to be lost with age, and aged toothless specimens are known (Thomson 1981, Ghasemzadeh 1998). There is a great variation in the shape of mullet teeth (ciliform, setiform, caniniform, bicuspid, tricuspid and multicuspid). The shape of the teeth and the pattern of dentition have been widely employed in taxonomic and systematic studies of mullets (Schultz 1946, Ebeling 1957, 1961, Thomson 1954b, 1975, 1997, Farrugio 1977, Menezes 1983, Ghasemzadeh 1998, Harrison and Senou 1999, Harrison et al. 2007).

Stomach Shape

Stomach and caeca can be seen by cutting the fish along the abdomen and removing the liver (Harrison and Senou 1999). As a general rule, the morphology of the stomach shows several differences between the Agonostominae and Mugilinae. It is a simple U-shaped sac of thin wall in the former, with the exception of the genus *Aldrichetta*, which exhibit thicker walls than in other Agonostominae (Thomson 1997). In Mugilinae, the stomach is usually divisible into a thin-walled cardiac crop and a very thick-walled biconical pyloric gizzard. This thick-walled, muscular stomach is a site of mechanical action used to break down algal cell walls. Bacteria, blue-green algae, diatoms and macroalgae that have been ingested with sand or other sedimentary material are triturated in this gizzard-like organ.

Head

The head as a whole is an informative organ from the taxonomic point of view, normally employed in any identification key of mullets. Although in mullets the head is often broad and flattened or gently convex dorsally, a wide variation in shape and relative size can be observed amongst the species of Mugilidae. The positional relationships among the different anatomical elements (jaws, nostrils, lips, eyes, opercular and preorbital bones, jugular space, etc.) and also their form (shape plus size), generates a variety of head shapes which can be used to aid taxonomic identification at the species level. At the geometric-morphometric level, many studies have discriminated species of mullets based on shape variables related to the head. For example, Heras et al. (2006) found that the one–two and one–four variables, which are inter-landmark distances belonging to the first box truss (that represents the head), were important measurements for the specific discrimination between *Mugil curema* and *M. cephalus*. These results agree with previous work (Ibáñez-Aguirre and Leonart 1996) where lineal morphometry, based on cephalic length and length to anal fin, differentiated both species. Moreover, González-Castro et al. (2012) found that the inter-landmark distances of the first box-truss, that represent the head shape, contributed significantly not only to the discrimination amongst seven species of the genus *Liza* and *Mugil* but also to plausible cryptic species of both *M. curema* and *M. cephalus* species complexes.

Mouth and Lips

The mouth in Mugilidae is normally of small/moderate size. It is terminal, although sometimes subterminal. The mouth gape is a ratio that has been employed in the past for taxonomic purposes. It is defined by Thomson (1997) as MW/ML, where: MW is the Mouth Width from mouth corner to mouth corner and, ML is the Mouth Length from the anterior tip of the lip to the posterior corner of the mouth opening.

Lips may be narrow or thick, smooth, lamellate or papillate. The upper lip may be terminal, or it may be overhung by a projection of the snout. The mouth features such as being terminal or subterminal, mouth gape, lips shape, dentition and ornamentation, and angle of dentary symphysis are all characters which have been used in taxonomy of mullets.

Jaws

In Mugilidae jaw structure is basically of the percoid type, distinguished by the premaxillary having short pedicels and a shaft which, in Agonostominae is widest at its mid-length and pointed at its distal end, whereas in the Mugilinae the shaft is broadest at the blade-like distal end (Thomson 1997, Ghasemzadeh 1998). In some genera of Mugilinae the edge of the premaxilla remains more or less parallel with the line of the mouth gape, but in others it curves down behind the corner of the mouth. The maxilla lies behind the premaxilla and at its upper end attaches to the ethmoid by a ligament. The degree of protrusibility of the mouth is largely governed by the degree of mobility of the maxilla, because they are locked to the premaxillary pedicels via the maxillary processes which also fuse in the midline. When the mouth is closed, the premaxillary pedicels retreat under the nasal bones (Thomson 1997). The maxillary and premaxillary bones may be almost straight as in most genera of Agonostominae, or may bend downwards posteriorly as

in members of the subfamily Mugilinae. When the latter occurs, the posterior end of the maxilla is usually visible when the mouth is closed (Thomson 1954a). This feature has been used by most taxonomists as a diagnostic character to identify some genera of mullets.

The anterior edge of the lower jaw consists of a pair of dentary bones which are joined together at the dentary symphysis. Each dentary bone has a horizontal arm which is edentulous or variably toothed, and another ventral arm with a fossa for the insertion and articulation of the angular bone (Ghasemzadeh 1998). The osteology of jaws has also been used by many authors in taxonomy and classification of mullets (Ishiyama 1951, Senou 1988, Ghasemzadeh 1998, Harrison 2002, Ghasemzadeh et al. 2004).

Preorbitals

The preorbitals are a pair of triangular bones, situated obliquely in front of the eyes. The anterior edge of these bones are elongate and denticulate, and depending on the genus or species of mullets may be notched, curved or straight (Ghasemzadeh 1998).

Nostrils

The nostrils may be variously placed in different species of mullets. In some species, the nostrils are nearer to each other than the posterior is to the eye or the anterior to the lip; in other species their position may be different (Thomson 1997). The posterior nostril usually reaches just above the level of the upper rim of the eye, but in a few species is higher. On the other hand, in *Rhinomugil squamipinnis* (Swainson) the posterior nostril is displaced to the level of the lower half of the eye (Thomson 1997).

Pharyngobranchial Organ

The structure of the pharyngobranchial organ (PBO) of Mediterranean mullet was studied by Capanna et al. (1974). They presented an account of its anatomy, histology, dentition and possible complex filtering function (for feeding on small benthic particles) with some photographic images of the skeletal components of the PBO. Harrison and Howes (1991) reviewed the PBO of mullet, and gave a detailed description of its structure, associated musculature and dentition, ontogeny, possible function, and its taxonomic utility among the genera of mullets.

Scales

Three types of scales can be observed in adult mullets: cycloid scales, as in *Myxus elongatus*, ctenoid scales, as in *Ellochelon vaigiensis*, and ctenoid scales with a digitated membranous hind border, as in *Valamugil* spp. The morphology and morphometry of scales has been employed for identifying genera, species and populations within Mugilidae (Ibáñez et al. 2007, Ibáñez et al. 2011).

Axillary and Obbasal Scales

The presence or absence of an axillary scale is another feature which is used in taxonomy of mullets. Thomson (1954a) defined the term axillary scale only for the elongated scale occurring at the base of the pectoral fins. He termed the elongated scales occurring at the base of the first dorsal and ventral fins as dorsal and ventral obbasals.

Meristic Characters

Number of Scales in the Lateral and Transverse Series

Traditionally, the number of scales in the lateral series (LI) can be counted over the left side of specimens, from the scale located just behind the head (i.e., immediately above the insertion of the pectoral fin) to the

caudal flexure (hypural plate limit). Its number varies approximately from 24 (*Ellochelon vaigiensis* or *Liza luciae*) to almost 63 in *Aldrichetta forsteri*. This meristic character is usually employed as a prominent diagnostic feature. However it is common to find overlapping scale counts in mullets at the intrageneric level (Thomson 1997, Ghasemzadeh 1998, Harrison 2002, González-Castro et al. 2008, González-Castro et al. 2012).

The transverse scale count (tr) can be interpreted as the number of scales between the origin of the first dorsal fin and the origin of the pelvic fin. However, some authors have used this count starting from the second dorsal fin to the origin of the anal fin base, which is less common. Transverse scale counts vary from eight to 10 (i.e., *Ellochelon vaigiensis*, *Liza grandisquamis* and *Liza luciae*), with a mode of 11 (some *Mugil*, *Liza* and *Valamugil* spp.), to a maximum value of 19 (*Aldrichetta forsteri*).

Number of Spines and Rays of Paired and Unpaired Fins

The first dorsal fin consists of four spines which is one of the most diagnostic characters of Mugilidae. Each spine is supported by a single basal pterygiophore. The first three spines are placed very close to each other, while the fourth spine is well-separated from them. The second dorsal fin consists of seven–10 rays in different genera of mullets, ranging from seven to eight rays in *Rhinomugil*; eight rays in *Mugil* and *Crenimugil*; nine rays in *Myxus*, *Trachystoma*, *Gracilimugil*, *Ellochelon*, *Liza*, *Paramugil* and *Valamugil*; nine to 10 rays in *Aldrichetta* and *Gracilimugil* and 10 rays in *Neomyxus* (Thomson 1997, Ghasemzadeh 1998). The anterior most ray of this fin is frequently mistaken for a spine. In fact it is a short and slender ray which is often unbranched and only segmented near its tip in adults (Ghasemzadeh 1998). The anal fin has three spines in most genera of mullets, except *Neomyxus* which has two spines and *Gracilimugil* which has three–four spines. The number of anal fin rays is eight in *Ellochelon*, *Rhinomugil* and some *Mugil* species; nine–11 rays in *Gracilimugil* and *Neomyxus* and some *Mugil*; 11–13 rays in *Aldrichetta* and nine rays in the rest of genera of Mugilidae (Ghasemzadeh 1998). Pectoral fins have one spine and 14–20 rays in different genera of mullets. Pelvic fins have the typical number of one spine and five rays.

Morphometric Differentiation of Mulletts

The Disadvantage of the ‘Size Effect’ in Morphometric Analysis: Influence of Size due to Allometric Growth

Most of the variability in a set of multivariate morphometric data from natural populations is due to individual size. In morphometrics, size must be considered as a contingent source of variability since it is associated with individual growth and the aim of such studies is usually focused on shape that must be size-free. In the general case of allometric growth (one type of ontogenetic variation), there is a variation in shape related to the variation in size (Leonart et al. 2000). Hence body size is usually a confounding factor in any morphometric analysis. When specimens under study belong to different populations, and especially to different age classes, then is to be expected that size generates an important bias in taxadiscrimination (González-Castro et al. 2007).

The influence of size due to allometric growth may be removed by appropriate statistical procedures (Gould 1966, cited in Leonart et al. 2000). There are numerous normalization methods whose aim is to eliminate the size effect in the context of allometric growth. However, some of the most popular methods have critical shortcomings that lead to misinterpretation of the results (Leonart et al. 2000). Among these, the ratio of every measurement to the one chosen as the independent variable effectively reduces all the individuals to the same size, but does not remove the undesired size effect because they maintain their size-dependent shape due to allometry. In other words, it is only valid if growth is isometric (i.e., shape does not change with size).

There are other methods to eliminate this size effect, such as ‘shearing’ (Humphries et al. 1981) or ‘Burnaby’s method for size correction’ (Burnaby 1966), which combine various techniques (i.e., regression) with a Principal Component Analysis (PCA) subsequently extracting the first principal component under the widespread view that this component represents the size in the PCA. However, it was observed that

both size and shape are embedded in the first component (Mosimann 1970, Sprent 1972, Humphries et al. 1981). Leonart et al. (2000) present a novel normalization-technique to scale data that exhibit an allometric growth. The method is theoretically derived from the equation of allometric growth. This normalization procedure is, consequently, compatible with allometry. It completely removes all the information related to size, not only scaling all individuals to the same size, but also adjusting their shape to that which they would have in their new size.

The normalization procedure of Leonart et al. (2000) has been employed successfully in several works related to Mugilidae taxonomy published in the last two decades (Ibáñez-Aguirre and Leonart 1996, Cousseau et al. 2005, Heras et al. 2006, González-Castro et al. 2008, González-Castro et al. 2012).

Different Kinds of Morphometric Variables and Different Morphometric Approaches

Linear Morphometric Measurements

Linear morphometric measurements (LMMs) are the ‘traditional’ measures employed on fishes. Among the most commonly in use in Mugilidae are: standard length (SL), head length (HL), head width (HW), snout length (Sn), pectoral fin length (PL), predorsal 1 distance (pD1d), predorsal 2 distance (pD2d), preventral distance (pVd), preanal distance (pAd), body height (BH) (Fig. 1.2).

Traditionally, LMMs were usually used to calculate ratios (i.e., percentages of some corporal variable over the total length), which were then employed to perform uni/multivariate analysis (without any consideration of the shape variation related to the size change). However, there are several biases and weaknesses inherent in traditional character sets: (1) Most characters tend to be aligned with the longitudinal axis, thus a large amount of the data are repetitious while other information (i.e., variation in oblique directions) is lacking; (2) Coverage of form is highly uneven by region as well as by orientation (dense in some areas of the body and sparse in others); (3) Some morphological points, such as the tip of the snout and the posterior end of the vertebral column, are used repeatedly. Any uncertainty in the positions of these morphological features will be propagated through a series of measurements; (4) Some LMMs are ‘extremal’ rather than ‘anatomical’ (i.e., greatest body depth), and therefore their placement may not be homologous from form to form; (5) Many measurements extend over much of the body. Long distances are usually employed in the traditional data sets, but are less informative than short ones (Strauss and Bookstein 1982, González-Castro 2007).

LMMs have proved to be useful however, if the size effect due to allometric growth is removed prior to the multivariate analysis. In this respect, the normalization procedure of Leonart et al. (2000), followed by multivariate analysis (PCA; Discriminant Analysis, DA), has been employed in some works related to taxonomy or comparative morphometrics of Mugilidae (Ibáñez-Aguirre and Leonart 1996, Cousseau

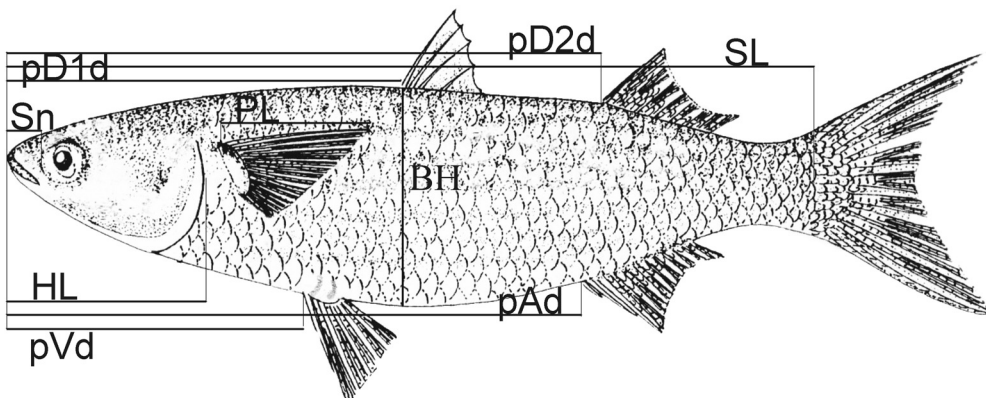


Figure 1.2. Linear morphometric measurements commonly employed on the morphological descriptions of the species of Mugilidae.

et al. 2005, Ibáñez-Aguirre et al. 2006, González-Castro et al. 2012) and also in studies related to growth analysis by means of morphometry (Minos et al. 1995, Ibáñez-Aguirre et al. 1999).

The use of morphometric characters to distinguish young stages of grey mullet species is a method with low accuracy due to major changes in body proportions (allometry), which occur in these stages (Thomson 1981). In this case, the use of the same body size of individuals of the compared groups (species) overcomes the problem, but the findings on this size are limited. According to Katselis et al. (2006) (who analyzed the variation in eight morphometric characteristics of the fry of four grey mullet species: *Liza aurata*, *Liza saliens*, *Chelon labrosus* and *Mugil cephalus*) "...this problem has been overcome with the use of the total length class of 20–35 mm for all species". According to DA classification, 92.7% of the specimens examined in this study were correctly classified into the four species.

Interlandmarks Distances Based on Box-Truss

Anatomical landmarks are true homologous points identified by some consistent feature of the local morphology. This implies that, when we establish a set of landmarks in two different forms to be compared (species, populations, morphs, etc.), by definition these landmarks must be located without any doubt in both morphs and have correspondence (biological homology) among forms (Bookstein 1991).

Strauss and Bookstein (1982) proposed a protocol for character selection, the truss network, which enforces systematic coverage of the form and largely overcomes the disadvantages of traditional data sets. This protocol systematically detects shape differences in oblique as well horizontal and vertical directions and archives the configuration of landmarks so that the form may be reconstructed (mapped) from the set of distances among landmarks (i.e., to obtain Cartesian coordinates for landmarks). Analyses of landmark data are usually based either on distance between selected pairs of landmarks or on the coordinates of the landmarks.

González-Castro (2007) (Fig. 1.3) and González-Castro et al. (2008, 2012) combined the Box-truss concepts of Strauss and Bookstein (1982), with the technique (for removing the influence of size due to allometric growth) of Lleonart et al. (2000) followed by multivariate analysis (PCA, DA), suggesting a new approach on the taxonomic analysis of mullets, but also of other fishes. This combination of methodologies represents a concise and low-cost way to successfully distinguish/discriminate species (or even populations) of Mugilidae.

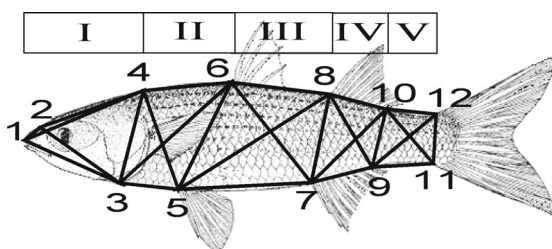


Figure 1.3. Box truss (Roman numerals) showing the interlandmark distances, based on 12 anatomical landmarks, proposed for the morphometric analysis of Mugilidae (from González-Castro 2007).

Coordinate Data

Morphometric techniques have ‘evolved’ in the last few decades in parallel with the introduction of promissory methods for archiving forms of organisms (Rohlf 1990). This discipline experienced a major revolution through the invention of coordinate-based methods, the discovery of the statistical theory of shape, and the computational realization of deformation grids (Mitteroecker and Gunz 2009). This new morphometric approach has been termed geometric morphometrics as it preserves the geometry of the landmark configurations throughout the analysis. Cartesian coordinates obtained from anatomical landmarks are the keystones on which geometric morphometrics are based. These coordinate data can come from

several sources, such as a digital camera, digitizing tablet or indirectly by reconstruction of landmarks from Box-trusses (Bookstein et al. 1985, Rohlf and Marcus 1993, González-Castro et al. 2012).

Corti and Crosetti (1996) performed the first geometric morphometric analysis on the grey mullet *Mugil cephalus*. Based on Partial Warps scores the authors described the shape differences and characterize 10 populations of this species, Galapagos being the most morphometrically distinct.

Ibáñez et al. (2007) performed a geometric morphometric analysis of fish scales for identifying genera, species and local populations within the Mugilidae. Fish scale form was least effective in discriminating populations from nearby areas, better when populations are more geographically dispersed, and best between species and genera. Scale form variation reflected previous genetic studies that differentiated congeneric *M. cephalus* and *M. curema*.

Recently, González-Castro et al. (2012) based on the Cartesian coordinates of 12 anatomical landmarks reconstructed from distance measurements among the landmarks (based on a Box-truss scheme) performed a geometric morphometric analysis of the body shape of six representative species of Mugilidae: *M. cephalus* Linnaeus 1758; *M. liza* Valenciennes 1836; *M. curema* Valenciennes 1836; *M. hospes* Jordan and Culver 1895; *Liza aurata* (Risso 1810); *L. ramada* (Risso 1826). Morphometry allowed discrimination not only among the six species, but also the American and European ‘populations’ of *Mugil cephalus* and the North and South American *Mugil curema*. Although some overlap among samples was detected, the DA (Cross-validated Discriminant Analysis) correctly classified 83.8% of the fishes according to their body shape.

The Barcode of Life Initiative as a Complementary-Genetic Tool for Non-Geneticist Mullet Taxonomists

Resolving species boundaries between closely related fish species, or families characterized by external uniformity (as in the Mugilidae is) is notoriously difficult. Such species can generally only be diagnosed based on few characters that often have a host of problems. For example, the morphological or meristic differences between these species may be very slight, difficult to describe and applicable only to a punctual ontogenetic stage. In the reverse situation, we can look at populations that are polymorphic with regard to characters that are normally diagnostic for species. The current trend in the field of taxonomy is defined as ‘integrative taxonomy’: to combine morphological and meristic analysis with newer disciplines, such as molecular genetics or geometric morphometrics (Dayrat 2005, González-Castro et al. 2008, Padial et al. 2010). Thus, it is possible to obtain comparable results, creating a synergistic effect and more robust conclusions. As was commented earlier in this chapter, mullet taxonomy is in a crisis. Overcoming this crisis is likely to be related to the integration of morphological/metric and molecular disciplines.

The use of a universally accepted short DNA sequence for identification of species (DNA barcoding or Barcode) has been proposed for application across all forms of life, within the Barcode of life Initiative. DNA barcoding may be an efficient aid to traditional taxonomy, designed to facilitate fast and accurate species identification (Hebert et al. 2003a,b, Hebert and Gregory 2005, Miller 2007). The fragment of 648 base pairs (bp) of the mitochondrial gene cytochrome c oxidase subunit 1 (COI) is the primary sequence of DNA barcoding for species of the animal kingdom (Hebert et al. 2003a). It is based on the premise that every species will probably have a unique DNA barcode and that genetic variation between species exceeds that within species (Hebert et al. 2003a,b). The primary goal of barcoding focuses on the assembly of reference sequence libraries derived from expert-identified voucher specimens in order to develop reliable molecular tools for species identification in nature.

Let us presume that on the date (September 2014), if we enter into the BOLD (Barcode of Life Data Systems) Public Data Portal (<http://www.boldsystems.org/index.php/>), and write ‘Mugiliformes’ in the link of ‘Taxonomy’, we will find the following information: 1149 published records, forming 112 BINs (clusters) related to 102 species with barcodes, with specimens from 43 countries, deposited in 37 institutions. Of these records, 893 have species names, and represent 83 public species. The Barcode Index Number

(BIN) system is a persistent registry for animal OTUs (Operational Taxonomic Units) recognized through sequence variation in the COI DNA barcode region. Since OTUs show high concordance with species, this system can be used to verify species identifications (Ratnasingham and Hebert 2013). Therefore, these data can give us an overview of the current state of the Barcode related to the taxonomy of Mugilidae. One hundred and twelve BINs suggest the existence of at least 112 species of Mugilidae already Barcoded, a record which is quite distant from the 72 species recognized by Nelson (2006) or the 71 species reported in Eschmeyer (2015) catalogue. We can also enter the public record list, download public sequences (in order to compare it with our sequences) and look at the record details for each specimen/sequence, or align the sequences and perform a Neighbour Joining Analysis.

Current Taxonomic Status and Conflicts in Fishes Belonging to the Mugilidae

Taxonomic Conflicts at the Generic Level

The Genera Chelon Artedi, 1793 and Liza Jordan and Swain, 1884

The generic name of *Chelon* is proposed on page 118 of an appendix to volume IV of the 1793 edition of Artedi's '*Synonymia nominum piscium*'. There is no description or type specimens mentioned and also no evidence whether the proposed names are binomial. Subsequently Jordan and Evermann (1917) designated *Mugil chelo* Cuvier 1829 as the possible type, and this was accepted by Schultz (1946), which according to Trewavas and Ingham (1972) is definitive, confirming the earlier tentative one. Trewavas and Ingham (1972) argued that since Röse (in: Walbaum 1793) cited pre-Linnaean names, the description and interpretation of subsequent authors like Rondelet and Gesner (in: Gudger 1934) apply at least mainly to *Mugil labeo* Cuvier. They also pointed out that these authors may also have confused *M. chelo* Cuvier with *M. labeo* in their description. Trewavas and Ingham (1972) also argued that if we accept that Röse's citations covering two species, even confusing the tautonomous name '*Chelo*' or '*Chelon*', the designation of type-species is left to a subsequent author, so according to the International Code of Zoological Nomenclature of 1961, Schultz's designation may be accepted.

Schultz (1946) however, included all the species belonging to the genera *Liza*, *Valamugil*, *Ellochelon* and *Oedalechilus* in *Chelon*. Earlier Oshima (1922) recognized the genus *Chelon* Röse, and assigned *Mugil crenilabis* (Forsskål 1775) to this genus. Schultz (1953) recognized *Oedalechilus* (Fowler 1903) as a valid genus, but still considered *Liza*, *Valamugil* and *Ellochelon* as synonymies of *Chelon*. Trewavas and Ingham (1972) considered *Mugil chelo* Cuvier 1829, as a synonym of *M. labrosus* Risso 1826, and concluded that the species of *Crenimugil* display closer affinity to *Chelon labrosus* than to species of *Liza*. Some authors like Taylor (1964), Senou (1988) and Randall (1995), have used the generic name of *Chelon* instead of *Liza*, without any explanation to elucidate their decision. Ghasemzadeh (1998), stated that the nomenclatural issue of date and authorship of *Chelon* and the confusion behind the history of the name is complex and should be addressed first, and the subject of whether *Chelon* is a synonym of *Liza* remains unresolved and requires more detailed taxonomic discussion.

Valamugil Smith, 1948 vs Moolgarda Whitley, 1945. Osteomugil?

Whitley (1945) established the genus *Moolgarda*. His generic description was based on an orthotype of *Moolgarda pura* which was probably a specimen of *Valamugil buchananai* or (unlikely) *V. cunnesius* which are abundant and frequently reported in coastal shallow waters of his type locality region (Point Cloates, western Australia). Whitley's description corresponds with *Valamugil* Smith 1948, especially his reference to the large pectoral axillary scales of the paired fins; obsolescent adipose eyefold, barely covering one third of the eye posteriorly, upper jaw terminal; upper lip moderately thick with microscopic cilia or entire, not papillose, jaws toothless; and also origins of second dorsal and anal fins about opposite each other, or anal fin slightly anterior. These characters are diagnostic for *Valamugil*. In the next paragraph Whitley mentioned that the closest group to the new genus was *Liza*. Whitley (1945) also compared Günther's (1861) description of *Mugil capito* Cuvier, as the genotype of *Liza*, with his Australian fish, and referred to

the hidden maxillary in his fish, which is another diagnostic character of *Valamugil*. Furthermore Whitley also observed some differences in the angle of the mandible, proportions of head and body, and scale counts, to propose a new genus for the Australian fish.

Whitley (1945) also suggested that two mainly eastern Australian species, '*Mugil*' *argenteus* Quoy and Gaimard, and *M. compressus* Günther, may tentatively be included in *Moolgarda*. He did not have any specimens of those two fishes at hand, and consulted Günther's (1861) description, which did not agree with the new genus. Therefore, his description was based on a species of *Valamugil*. Unfortunately, no type specimen of *Moolgarda pura* was retained in either the Australian Museum, the western Australian Museum, or another institution, and most authors use *Valamugil* Smith 1948, instead of *Moolgarda* Whitley 1945, which is reasonable according to the zoological code.

Luther (1977) studied some genera and species of Indian mullets using osteology of the vertebral column, degree of adipose eyelid development on the orbit, visibility of the end of maxilla and number of pyloric caeca. He erected the new genus *Osteomugil* based on a single specimen of *Mugil cunnesius* Valenciennes 1836. In his remarks Luther (1977) stated that his new genus has some affinity to *Valamugil*. Subsequent studies by Thomson (1997), Senou (1988) and Ghasemzadeh (1998) proved the synonymy of *Osteomugil* with *Valamugil*.

Taxonomic Conflicts at the Species Level

The Mugil curema Species Complex and Mugil rubrioculus nova sp.

The white mullet *Mugil curema* Valenciennes 1836 is a widely distributed mullet. This species inhabits the Pacific coast of America from the Gulf of California to North Chile; and the Atlantic coast of America from Cape Cod to Argentina and the west coast of Africa from Gambia to the Congo (Menezes 1983, Thomson 1997, Harrison 2002, González-Castro et al. 2006).

Mugil curema was 'traditionally' considered a conspicuous species, well differentiated from its congeners by its meristic counts and morphological characters. However, some taxonomic confusion has occurred during the last four decades in both North and South America, as evidenced by the long discussions which arose around them, the validity or synonymy of *Mugil gaimardianus* Desmarest 1831, *Mugil brasiliensis* Günther 1861 (currently both invalid species), *Mugil rubrioculus* sp. nov. (Harrison et al. 2007) and its taxonomic/morphological relationship with the white mullet *Mugil curema* (Alvarez-Lajonchere 1975, Menezes 1983, Godinho et al. 1988, Cervigón 1993, Nirchio et al. 2003, Harrison et al. 2007). Moreover, some inconsistencies between the identification keys and the field characters have been observed for specimens of the white mullet around the American continent (Menezes 1983, González-Castro et al. 2006, M. González-Castro, pers. comm.).

It was in the last decade that some work shed light on this apparent taxonomic uncertainty: *Mugil curema* is undoubtedly a species complex (Nirchio and Cipriano 2005, Heras et al. 2006, Fraga et al. 2007, Heras et al. 2009, Durand et al. 2012a). This haplogroup is apparently monophyletic (Durand et al. 2012b), but it includes *Mugil incilis*, which is easily meristically and morphologically identifiable from *Mugil curema* (Thomson 1997, Harrison 2002). The *Mugil curema* species complex would be constituted by at least four lineages, which include three different karyotypes (more information is given in Chapter 15—Rossi et al. 2015). Interestingly, in an assessment of lineal versus landmark-based morphometry for discriminating species of Mugilidae, González-Castro et al. (2012) showed that the three morphometrics approaches employed separated *M. curema* specimens in two groups (Argentinean and Mexican samples), suggesting they may constitute different species. The variables (interlandmarks distances) responsible for these differences were mostly located in the head (Box-truss I) and in the segment of the body delimited by the ventral, first/second and anal fins (Box-trusses III and IV) (Fig. 1.3). On the other hand, meristic counts do not show significant differences between both groups (González-Castro et al. 2012) and instead, the colouration pattern seems to be useful in order to contribute to the specific determination of this species complex (González-Castro et al. 2006, Harrison et al. 2007, M. González-Castro, pers. comm.).

Harrison et al. (2007) presented karyological and morphological evidence for a mullet in Venezuelan coastal waters that does not conform to the description of any other species from the western central Atlantic

and has the feature of a red eye that was often used by earlier authors to define nominal *M. gaimardianus*. These authors establish a valid name for the species, *Mugil rubrioculus* n. sp. Surprisingly, Durand et al. (2012a), found a phylogroup of the *Mugil curema* species complex which has $2N = 48$ (the same number of chromosomes as *Mugil rubrioculus*). *Mugil rubrioculus*, *Mugil hospes* and the *Mugil curema* species complex (including *M. incilis*) would constitute one of the two Sub-Clades of the monophyletic genus *Mugil*, according to Heras et al. (2009) and Durand et al. (2012a). In the future, much work should be done in order to morphologically differentiate, and assign a specific name to, each of the remaining three lineages of the *Mugil curema* species complex.

Mugil cephalus: The Biggest Species Complex of Mugilidae, or Just a Cosmopolitan Species?

The flathead mullet *Mugil cephalus* Linnaeus 1758 is the type species of the genus *Mugil* and undoubtedly the most studied mullet. A recent global review of this species concentrated on the biology, genetics, ecology and fisheries aspects (Whitfield et al. 2012). *Mugil cephalus* is the most widespread species of the Mugilidae: the species has been recorded in coastal and estuarine waters of temperate, subtropical and tropical regions, mainly between latitudes 42°N and 42°S (Thomson 1997, Harrison 2002, Nelson 2006, González-Castro et al. 2008, Durand et al. 2012a, Whitfield et al. 2012).

Despite its global spread in both hemispheres, *M. cephalus* has a discontinuous distribution. Questions regarding its taxonomic status have been raised in many genetic studies, most of which suggest *Mugil cephalus* is a species complex (Crosetti et al. 1994, Rossi et al. 1998a, Rocha-Olivares et al. 2000, Fraga et al. 2007, González-Castro 2007, González-Castro et al. 2008, Heras et al. 2009, Jamandre et al. 2009). Recently, Durand et al. (2012a) postulated that a *Mugil cephalus* species complex would be constituted by 14 parallel lineages that included the *M. liza* lineage and 13 other lineages, all currently designated as *M. cephalus*. Generally, each lineage has a regional distribution, whereas in some instances, different lineages co-exist at a single locality. Shen et al. (2011) recorded three lineages for Taiwan; another example is New Caledonia where two lineages were sampled, one of which was also sampled in New Zealand, the other one (L3) also occurred in Fiji and Taiwan (Durand et al. 2012a).

The huge number of results obtained strongly suggest that the ‘*Mugil cephalus* species-complex’ is comprised of at least 14 biological species, including the mitochondrial lineage of *M. cephalus* (Linnaeus 1758) sampled in the Mediterranean (the type-locality), and *M. liza* (for further details and discussion see Chapter 2—Durand 2015 and Chapter 15—Rossi et al. 2015). To delimit, describe and give scientific names to these cryptic species could be the biggest challenge facing the taxonomy of mullets.

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CHAPTER 2

Implications of Molecular Phylogeny for the Taxonomy of Mugilidae

Jean-Dominique Durand

“La première famille dont nous traçons l’histoire dans ce volume est une de celles qui nous ont donné le plus de peine, à M. Cuvier et à moi.”

“... la similitude, on peut dire désespérante, de tous ces poissons, attache à leur synonymie et à l’expression de leurs caractères des difficultés tout aussi insurmontables...”

Cuvier and Valenciennes 1836

Introduction

Since the first attempt at Mugilidae systematics by Cuvier and Valenciennes (1836), the number of species and genera, and their phylogenetic relationships, have been constantly debated. In successive revisions, an increasing number of morpho-anatomical traits have been considered. The profound morpho-anatomical similarity of Mugilidae species, and the difficulty of interpreting anatomical differences from an evolutionary perspective, render the situation very complex in terms of making phylogenetic inferences and clearly identifying species and genera. As a result, there is no consensus on Mugilidae systematics, and taxonomic inconsistencies persist (see Chapter 1—González-Castro and Ghasemzadeh 2015).

Genetic polymorphisms constitute a valid and powerful alternative to morphology that can be used to test the prevailing phylogenetic assumptions based upon morphological traits. Early applications of genetics to Mugilidae had this objective, of resolving taxonomic problems with species identification and phylogenetic relationships. The first study used karyotype similarities, and variables such as the number of chromosomes and the position of their centromere (Cataudella et al. 1974), to investigate the validity of Mugilidae genera in the Mediterranean Sea. The Mediterranean mullet species had the same number of chromosomes ($2n = 48$), but their morphology differed, leading Cataudella et al. (1974) to group species under three cytotaxonomic categories that were largely consistent with the taxonomy based on anatomical traits. Subsequent cytogenetic studies also identified $2n = 48$ chromosomes in Mugilidae (for a review Rossi et al. 1996) except in *Mugil curema* whose populations in the USA and Brazil have $2n = 28$ chromosomes (LeGrande and Fitzsimons 1976, Cipriano et al. 2002, Nirchio et al. 2005) and $2n = 24$ in Venezuela (Nirchio and Cequea 1998, Nirchio et al. 2001, 2003). Even though such cytogenetic

features question the taxonomic status of these populations, no definitive conclusions could be made (Rossi et al. 2005).

Later cytogenetic techniques were improved by staining and fluorescent *in situ* hybridization (FISH) with several types of DNA probes, which permitted observation of finer features such as the Nucleolus Organizer Regions (NORs) (reviewed in Sola et al. 2007). This technique was used to investigate geographic variation of genetic differentiation of *Mugil cephalus* (Rossi et al. 1996) and phylogenetic relationships among Mugilidae species (for a review see Sola et al. 2008). No cytogenetic polymorphisms were observed among worldwide samples of *M. cephalus* (Rossi et al. 1996), whereas variations in the location of genes for 18S rRNA and 5S rRNA, and the composition of the constitutive heterochromatin, were observed among the previous cytotypes of Mugilidae species (Sola et al. 2008). These cytogenetic features were used to reconsider cytotaxonomic relationships, but evolutionary interpretation of the variation in these traits was still dependent upon prevailing morpho-anatomical hypotheses.

In the same period, allozyme electrophoresis was used to identify species (Herzberg and Pasteur 1975, Callegarini and Basaglia 1978) and, by increasing loci and tissues, the phylogenetic relationships among species (Autem and Bonhomme 1980, Menezes et al. 1992, Rossi et al. 1998a, Papisotiropoulos et al. 2001, Rossi et al. 2004, Turan et al. 2005, Blel et al. 2008). This finally led to analysis of the genetic diversity/population structure of *Mugil cephalus* (Campton and Mahmoudi 1991, Rossi et al. 1998b, Huang et al. 2001). With few exceptions (Menezes et al. 1992, Lee et al. 1995, Liu et al. 2010, Rossi et al. 1998a), all phylogenetic investigations were exclusively focused on Mediterranean species, which greatly limited their impact for understanding the systematics of the family. The low levels of genetic polymorphism that are typically recovered with allozyme loci however prevented the application of these techniques to wider species sampling.

The extensive development of Polymerase Chain Reaction (PCR) methods in the 1990s allowed the most significant advance in Mugilidae systematics. The PCR methods greatly facilitated access to DNA sequence polymorphisms, providing direct insights into the evolutionary history of families and species. Initial molecular phylogenetic studies were limited to a single sequence portion of a gene, with the objective of clarifying phylogenetic relationships among Mediterranean mullet species (Caldara et al. 1996, Rossi et al. 2004, Papisotiropoulos et al. 2007, Imsiridou et al. 2007, Erguden et al. 2010). Later studies were extended to more gene portions and other species of Mugilidae (Fraga et al. 2007, Semina et al. 2007, Aurelle et al. 2008, Heras et al. 2009, Liu et al. 2010, Durand et al. 2012a, Siccha-Ramirez et al. 2014, Xia et al. submitted). Molecular techniques were also used to investigate species boundaries and population genetic structure (Crosetti et al. 1993, 1994, Rocha-Olivares et al. 2000, 2005, Heras et al. 2006, Liu et al. 2007, Liu et al. 2009, Jamandre et al. 2009, Ke et al. 2009, Jamandre et al. 2010, Shen et al. 2011, Sun et al. 2012, Durand et al. 2013, Krüeck et al. 2013, McMahan et al. 2013, Mai et al. 2014). All these studies shed new light on the phylogeny and diversity of the Mugilidae, leading some authors to propose large revisions of their taxonomy (Durand et al. 2012b, Xia et al. submitted). This revision of Mugilidae taxonomy, based on the results of molecular phylogenetic and population genetic studies, is presented in the following sections. The Mugilidae diversity consists of more than 91 mitochondrial lineages, corresponding to 53 morphological species and 38 putative species, which form 25 genera, five tribes and four subfamilies.

Impact of Recent Molecular Phylogeny on Taxonomy

Subfamilies

The inference of systematic relationships of the family based upon morpho-anatomical characters has led to conflicting hypotheses (see Fig. 1 in Durand et al. 2012a). The only area of agreement concerned the phylogenetic position of the genera *Agonostomus* and *Joturus*, usually presented as basal in all phylogenies (Schultz 1946, Senou 1988, Harrison and Howes 1991, Thomson 1997, Ghasemzadeh 1998). Some authors included *Cestraeus* and *Aldrichetta* among these plesiomorphic genera (Harrison and Howes 1991, Thomson 1997, Ghasemzadeh 1998) forming the subfamily Agonostominae *sensu* Thomson (1997); all other species belong to the subfamily Mugilinae *sensu* Thomson (1997).

The first comprehensive molecular systematics of the Mugilidae, using phylogenetic analyses of nucleotide sequence variation at three mitochondrial loci, highlighted seven major lineages that radiated early, to all current forms, from a common ancestor (Durand et al. 2012a). While *Joturus*, *Agonostomus* and *Cestraeus* belonged to a unique lineage, they are also closely related to genera of more recent origin in phylogenies based upon morpho-anatomical characters, such as *Mugil*, *Chaenomugil*, *Myxus* and *Neomyxus*. The low resolution of deep nodes of the tree, however limits phylogenetic interpretations and tests of morpho-anatomical hypotheses. Recently, Xia et al. (submitted) used additional loci (mitochondrial and nuclear) to gain better resolution of the phylogenetic tree (Fig. 2.1). They demonstrated that Mugilidae genera belong to four clades, considered to represent subfamilies (Xia et al. submitted). These subfamilies were identified by the combination of six morpho-anatomical traits: 1. the scale type for all or a majority of body scales, 2. the position of the pelvic fin tip relative to the first dorsal fin, 3. the position of the jaw end relative to the mouth gape (JM), 4. the shape of the preorbital frontal edge, 5. the number of pyloric caeca and 6. the maxilla below the mouth corner when the mouth is closed.

Myxinae Xia, Durand and Fu submitted

Type Genus. *Myxus* Günther, 1861

The Myxinae subfamily *sensu* Xia et al. (submitted) is composed of two monotypic genera, *Myxus* and *Neomyxus*. This subfamily is basal in the phylogenetic tree suggesting that the two genera are the most plesiomorphic. This contrasts with the general conclusion of reviews based on morpho-anatomical traits, such as Harrison and Howes (1991), which considered the morphology of the Pharyngo-Branchial Organ (PBO) of *Myxus* and *Neomyxus* as one of the most derived. Beyond the molecular evidence, this subfamily is characterized by the following combination of diagnostic morpho-anatomical traits: cycloid scales, a pelvic fin tip that barely reaches the vertical from first dorsal fin origin, upper jaw position above the line of mouth gape, presence of only two pyloric caeca.

This subfamily is endemic to the Pacific, occurring along the eastern coast of Australia and in the central Pacific.

Mugilinae Xia, Durand and Fu Submitted

Type Genus. *Mugil* Linnaeus, 1758

The new-recombined Mugilinae subfamily *sensu* Xia et al. (submitted) is composed of six genera: *Mugil*, *Chaenomugil*, *Agonostomus*, *Dajaus*, *Joturus* and *Cestraeus*. The genus *Cestraeus* is the most divergent while other genera belong to two evolutionary lineages: one consisting of *Joturus*, *Dajaus* and *Agonostomus* and a second consisting of *Mugil* and *Chaenomugil* (Fig. 2.1). With the exception of *Aldrichetta*, all genera considered as plesiomorphic by Thomson (1997) and assigned to the Agonostominae subfamily fall within this molecular subfamily. Despite this congruent result, the presence in this clade of the genera *Mugil* and *Chaenomugil* justified the new recombination of the subfamily Mugilinae. Beyond the molecular evidence, this subfamily is characterized by a combination of ctenoid scales (with the exception *Mugil capurii*), a pelvic fin tip that reaches the vertical from spines I–IV of the first dorsal fin, a shape of the preorbital front edge that is not notched, presence of only two pyloric caeca and the maxilla below the mouth is not visible when the mouth is closed (Xia et al. submitted). The Mugilinae subfamily occurs in all tropical and subtropical waters of the world, but with a phylogenetic diversity that is higher along the shores of the Americas.

Rhinomugilinae Xia, Durand and Fu submitted

Type Genus. *Rhinomugil* Gill, 1863

The Rhinomugilinae subfamily *sensu* Xia et al. (submitted) comprises 11 genera that belong to four evolutionary lineages, considered as tribes by Xia et al. (submitted) (Fig. 2.1). This subfamily is

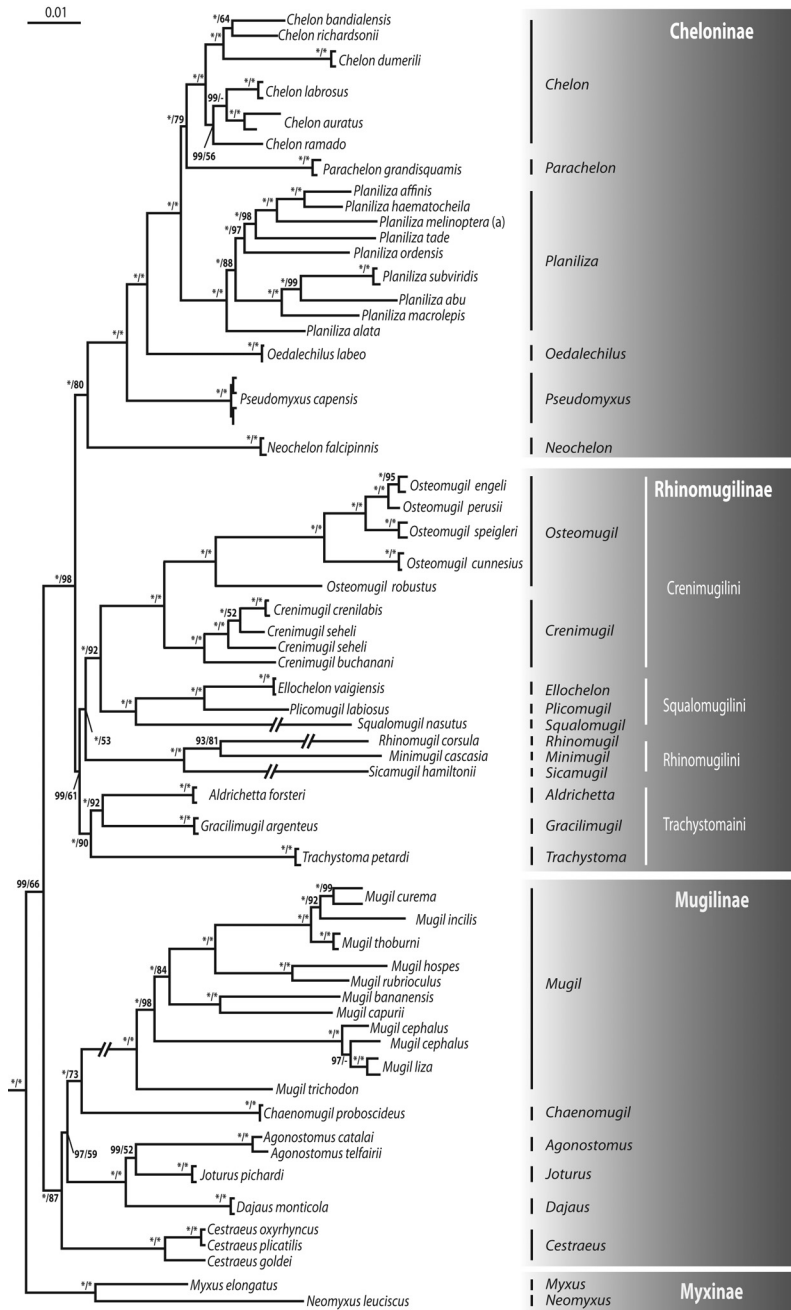


Figure 2.1. Phylogenetic tree depicting relationships among major lineages within the Mugilidae.

Relationships were inferred using partitioned Bayesian and maximum likelihood (ML) analyses of 12,945 bp un-ambiguous sequences from twelve nuclear loci (9,843 bp) and three mitochondrial genes (3,102 bp) (Xia et al. submitted). With exception of *Mugil*, *Sicamugil hamiltonii*, *Rhinomugil corsula* and *Squalomugil nasutus*, branch length is proportional to the number of substitutions under an optimal substitution model for each partition of concatenated mitochondrial and nuclear gene data (provided in Xia et al. submitted). Numbers on the branches are Bayesian posterior probabilities for the Bayesian analyses and ML bootstrap values (in %, from 1000 replicates). Asterisks indicate nodes with a posteriori probability from partitioned Bayesian analysis of 1 and a ML bootstrap of 100%, ‘-’ indicate that the ML bootstrap value is less than 50%. Out-group taxa are not shown. (a) correspond to the specimen MNHN-IC-2011-0212 named *Paramugil parmatus* in Durand et al. (2012a) but re-identified by Ghasemzadeh as *Planiliza melinoptera*. In white, subfamilies and tribes names proposed by Xia et al. (submitted).

phylogenetically closer to the Cheloninae *sensu* Xia et al. (submitted) and presents wide morpho-anatomical diversity that precludes the identification of diagnostic morpho-anatomical traits. This subfamily occurs in the Indo-Pacific and is divided into four tribes.

Trachystomaini Xia, Durand and Fu Submitted

The Trachystomaini tribe consists of three monotypic genera: *Trachystoma*, *Gracilimugil* and *Aldrichetta*. The short length of mucus canals on scales is the main characteristic of this tribe within the Rhinomugilinae subfamily. This tribe occurs exclusively in the South West Pacific.

Rhinomugilini Xia, Durand and Fu Submitted

The Rhinomugilini tribe consists of three monotypic genera: *Rhinomugil*, *Sicamugil* and *Minimugil*. It is differentiated from all other tribes by the following combination of morpho-anatomical traits: two pyloric caeca, no scale free area on the top of the head, and absence of endopterygoid teeth. This tribe occurs in freshwaters of India, Bangladesh and Myanmar.

Squalomugilini Xia, Durand and Fu Submitted

The Squalomugilini tribe consists of three genera: *Squalomugil*, *Plicomugil* and *Ellochelon*. This tribe is differentiated from all others by possessing four or more pyloric caeca (more than 14 in *Ellochelon* and *Squalomugil*), an emarginated or truncated caudal fin, a second dorsal fin origin at vertical $\geq 2/3$ along the anal fin base. This tribe occurs in the Indian Ocean and the West Pacific.

Crenimugilini Xia, Durand and Fu Submitted

The Crenimugilini tribe consists of two genera: *Crenimugil* and *Osteomugil*. All members of this tribe have distinctive long pectoral axillary scales, and scales with a membranous, digitated hind margin (Fig. 2.2). It is widely distributed in the Indo-Pacific.

Cheloninae Xia, Durand and Fu Submitted

Type Genus. *Chelon* Artedi, 1793

The subfamily Cheloninae comprises six genera: *Neochelon*, *Oedalechilus*, *Pseudomyxus*, *Planiliza*, *Parachelon* and *Chelon*. All genera are considered of recent origin in phylogenies based on morpho-anatomical traits (Schultz 1946, Harrison and Howes 1991, Thomson 1997). This is in agreement with the molecular phylogeny; this subfamily and the Rhinomugilinae are the most recently diverged (Xia et al. submitted). Within the Cheloninae, the genus *Neochelon* is the most divergent, followed by *Pseudomyxus* and then *Oedalechilus*. *Planiliza*, *Parachelon* and *Chelon* diverged more recently from a common ancestor (Fig. 2.1). The Cheloninae subfamily is characterized by ctenoid scales (with the exception of *Neochelon* and *Pseudomyxus*), a pelvic fin tip that reaches the vertical from spines I–IV, a jaw end below the line of mouth gape, a preorbital front edge that is notched, a number of pyloric caeca > 14 , and a maxilla below the mouth corner that is visible when the mouth is closed. This subfamily occurs in the East Atlantic, in the Mediterranean Sea and the Indo-Pacific. It is absent from American continental waters (East Pacific, West Atlantic).

Genera

Cuvier and Valenciennes (1836) produced the first major taxonomic study of the Mugilidae, based on a major worldwide sampling. They assigned Mugilidae to four genera: *Mugil*, *Dajaus*, *Cestraeus* and *Nestis*.

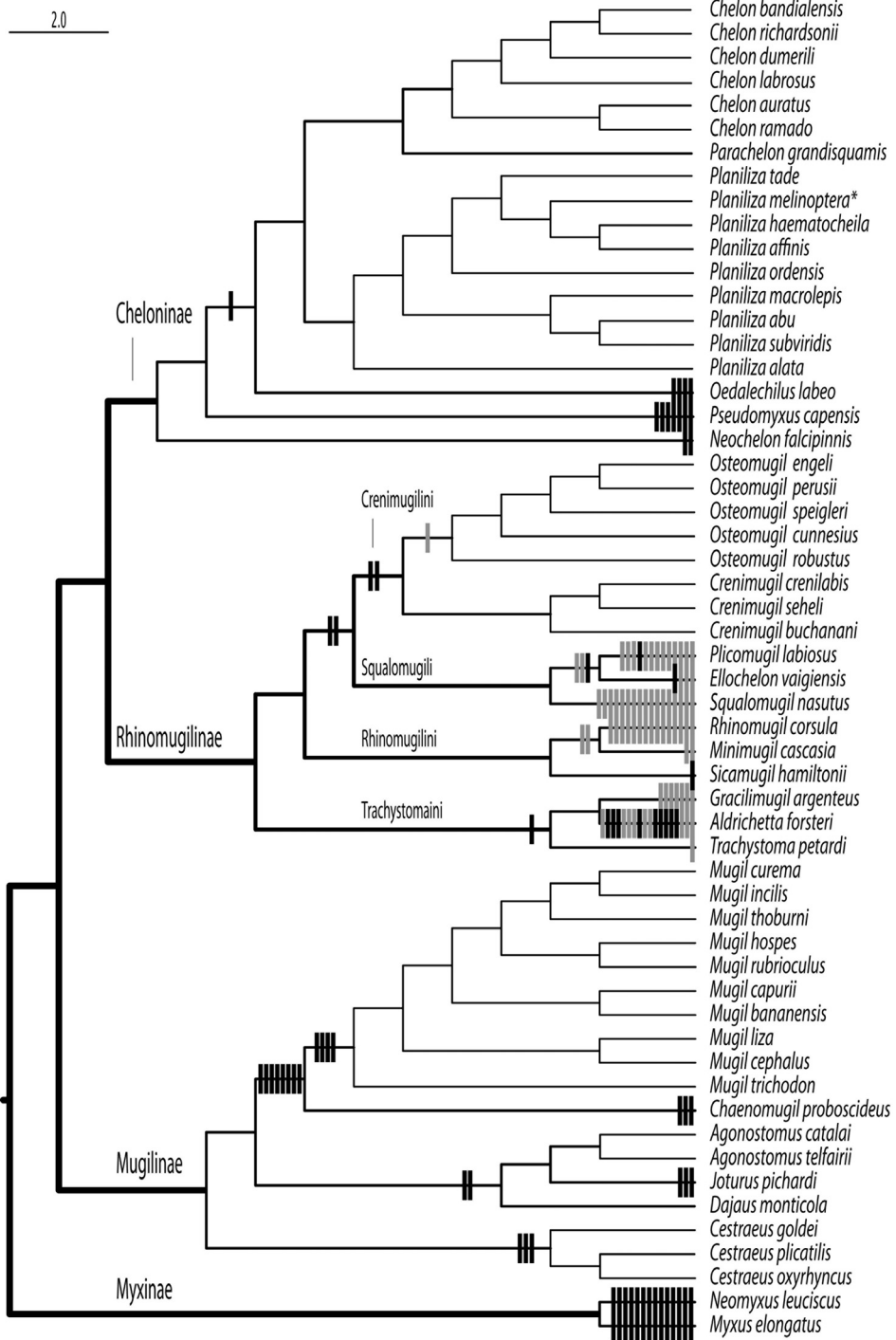


Figure 2.2. Diagnostic morpho-anatomical characters in subfamilies, tribes and genera of the Mugilidae family.

There were highlighted among 68 morpho-anatomical traits inferred on the basis of the likelihood reconstruction of ancestral character state using Mesquite 2.75 (Maddison and Maddison 2011, Xia et al. submitted). Bars correspond to diagnostic traits of genera belonging to the same subfamily (black bars) or tribe (grey bars). Branch thickness corresponds to the taxonomical ranks: subfamily, tribe, genus, species. * corresponds to the specimen MNHN-IC-2011-0212 named *Paramugil parmatus* in Durand et al. (2012a) but re-identified by Ghasemzadeh as *Planiliza melinoptera*.

Later, Günther (1861) only accepted three genera as valid based upon the presence and disposition of the teeth: *Mugil*, *Agonostoma* and *Myxus*; *Nestis* and *Dajaus* being junior synonyms of *Agonostoma*. After these initial classifications, new genera were continuously described, up to 30, before the taxonomic revision proposed by Schultz (1946). Based upon mouth anatomy, Schultz (1946) reduced the number of genera to 13, while Smith (1948) recognized 16. Later, Schultz (1953) reaffirmed the validity of 13 genera and described one more. In 1988, Senou listed 15 genera that were only partially consistent with those previously accepted, while describing three new ones. None of these new genera were considered in subsequent classifications, including those provided by Harrison and Howes (1991), Thomson (1997) or Ghasemzadeh (1998). Among these, discrepancies remained concerning nomenclature and phylogenetic relationships inferred from morpho-anatomical traits. It was in this context that Durand et al. (2012a) and, more recently, Xia et al. (submitted), investigated phylogenetic relationships using DNA sequence polymorphisms. These molecular phylogenies, using a large sample of species representative of global Mugilidae diversity, permitted tests of morpho-anatomical assumptions and, more importantly, proposed a revised classification, as described below.

Agonostomus Bennett, 1832

Type species. *Agonostomus telfairii* Bennett 1832 (holotype BMNH 1861.8.14.9). Mauritius, Mascarenes, South-western Indian Ocean.

All molecular phylogenetic reconstructions, using either mitochondrial or a combination of mitochondrial and nuclear gene polymorphisms, have highlighted the paraphyly of *Agonostomus* with respect to *Joturus* (Durand et al. 2012a,b, Xia et al. submitted, Fig. 2.1). Because the type species of the genus *Agonostomus* is the South-West Indian species *A. telfairii*, Durand et al. (2012b) suggested placing American *Agonostomus* species under a different genus name, namely *Dajaus*, to conserve the monotypic genus *Joturus*. This suggestion is in agreement with Cuvier and Valenciennes (1836). *Dajaus* is the brother genus of *Joturus* and *Agonostomus* inside the Mugilinae subfamily (Xia et al. submitted, Fig. 2.1). There are no morpho-anatomical synapomorphies that characterize *Agonostomus* and *Dajaus* genera, but their allopatric distributions and phylogenetic positions argue for the validity of the two genera. *Agonostomus* comprises two species *A. telfairii* and *A. catalai* and occurs exclusively in the South West Indian Ocean (Comores, Mayottes, Madagascar, Réunion and Mauritius).

Aldrichetta Whitley, 1945

Type species. *Mugil forsteri* Valenciennes 1836. No types known.

All molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with a taxonomy based on morphological and anatomical traits (Eschmeyer and Fong 2014). The *Aldrichetta* genus is monotypic and the brother genus of *Gracilimugil*, part of the Trachystomainsi tribe inside the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). *Aldrichetta* is supported by 19 diagnostic morpho-anatomical traits, 10 of which are at the subfamily rank: jaw end on line of gape, preorbital front edge not notched, mid-gape at level of or below lower rim of the eye, nine soft rays in the second dorsal fin, 58 or more scales in the longitudinal series, 18 or more scales in the transverse series, 18 or more scales in the longitudinal series reached by the tip of the pectoral fin when laid back, 19 or more scales between the operculum and the vertical from the origin of the first dorsal fin, 37 or more scales between the operculum and the vertical from the origin of the second dorsal fin (Xia et al. submitted, Fig. 2.2). It is restricted to the temperate coastal waters of Australia and New Zealand (Thomson 1997).

Cestraeus Valenciennes, in Cuvier and Valenciennes, 1836

Type species. *Cestraeus plicatilis* Valenciennes, in Cuvier and Valenciennes 1836 (holotype MNHN A-2894). Sulawesi, Indonesia.

All molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with the taxonomy based on morphology and anatomy (Eschmeyer and Fong 2014). The *Cestraeus* genus is represented by three species: *Cestraeus goldiei* Macleay 1883, *Cestraeus oxyrhynchus* Valenciennes, in Cuvier and Valenciennes 1836, and *Cestraeus plicatilis* Valenciennes, in Cuvier and Valenciennes 1836. It belongs to the Mugilinae subfamily *sensu* Xia et al. (submitted, Fig. 2.1) and it is supported by three diagnostic morpho-anatomical traits: fleshy lobes over end of upper jaws, mid-gape at level of or below lower rim of eye, 20 to 21 rays in the pectoral fin (Thomson 1997, Xia et al. submitted, Fig. 2.2). The genus *Cestraeus* is present in the Indo-Malay-Papua archipelago, in New Caledonia and in Fiji (Thomson 1997).

Chaenomugil Gill, 1863

Type species. *Mugil proboscideus* Günther 1861 (syntype BMNH 1860.7.21.22). Pacific coast of Central America.

All molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with the taxonomy based on morphological and anatomical traits (Eschmeyer and Fong 2014). The *Chaenomugil* genus is monotypic and the brother genus of *Mugil*, inside the Mugilinae subfamily *sensu* Xia et al. (submitted, Fig. 2.1). In its subfamily, it is characterized by three diagnostic morpho-anatomical traits: edge of the lower lip permanently turned down, mouth corner reaching vertical from anterior nostrils or a little behind, first dorsal fin origin nearer caudal base than to snout tip (Thomson 1997, Xia et al. submitted, Fig. 2.2). *Chaenomugil* occurs in the eastern Pacific, from Baja California to Peru (Thomson 1997).

Chelon Artedi, 1793

Type species. *Mugil chelo* Cuvier 1829 (lectotype MNHN 0000-6400, paralectotypes: MNHN A-3588 to 3589; A-3596; A-3599; A.3602 to 3603; A-3775; A-4651; A-4693; A-4697). Brest, France.

Phylogenetic reconstructions based on genetic data have provided contrasting views of phylogenetic relationships between the genera *Liza* and *Chelon*. While *Chelon* and *Liza* species belong to two different clades disputing the validity of these genera (Autem and Bonhomme 1980, Papatotiroopoulos et al. 2001, Murgia et al. 2002, Blel et al. 2008), others studies have pointed out the paraphyly of the genus *Liza* with *Chelon* (Caldara et al. 1996, Papatotiroopoulos et al. 2002, Rossi et al. 2004, Turan et al. 2005, Gornung et al. 2007, Imsiridou et al. 2007, Papatotiroopoulos et al. 2007, Aurelle et al. 2008, Heras et al. 2009). However, these studies were usually limited to few species (Mediterranean ones) or based on allozyme markers with limited variation. Recent molecular phylogenies based on large species samples (Durand et al. 2012a,b) or numerous mitochondrial and nuclear sequence polymorphisms (Xia et al. submitted) have clearly demonstrated the paraphyly of both *Liza* and *Chelon* genera (Durand et al. 2012a,b, Xia et al. submitted). Considering the phylogenetic tree and the position of *Chelon* and *Liza* type species *Mugil chelo* and *Mugil capito* (currently *C. ramado*) respectively, Durand et al. (2012b) synonymized *Liza* with *Chelon*, resurrected *Gracilimugil* and *Planiliza* (see hereafter) and created three new genera. *Chelon* is the brother genus of genera *Parachelon* and *Planiliza* (Fig. 2.1) and consists of at least nine species (see hereafter and Chapter 6): *C. auratus*, *C. bandialensis*, *C. bispinosus*, *C. dumerili*, *C. labrosus*, *C. ramado*, *C. richardsonii*, *C. saliens*, and *C. tricuspidens*. No diagnostic morpho-anatomical traits has been highlighted in *Chelon*, among other genera belonging to the subfamily Cheloninae (Xia et al. submitted). This genus occurs exclusively in temperate and tropical waters of the East Atlantic Ocean, Mediterranean Sea and the temperate waters of South Africa.

Crenimugil Schultz, 1946

Type species. *Mugil crenilabis* Forsskål 1775. No types known.

Molecular phylogenetic reconstructions based on mitochondrial sequences (Durand et al. 2012a) or a combination of mitochondrial and nuclear gene sequences (Xia et al. submitted), both highlighted the paraphyly of *Moolgarda* and *Valamugil* with *Crenimugil*. Based upon the fact that *Moolgarda* is both a *nomen nudum* and a *nomen dubium* (Thomson 1997; for more details see Ghasemzadeh 1998), and the principle of priority, Durand et al. (2012b) synonymized *Moolgarda* and *Valamugil* with *Crenimugil*. *Crenimugil* is the brother genus of *Osteomugil*, part of the Crenimugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). *Crenimugil* consists of three nominal species: *C. crenilabis*, *C. buchanani* and *C. seheli* but the species diversity of this genus is probably strongly underestimated (see hereafter, Table 2.1). No diagnostic morpho-anatomical traits were revealed when 68 morpho-anatomical characters were plotted onto the molecular phylogenetic tree (Xia et al. submitted, Fig. 2.2). The genus *Crenimugil* has a wide Indo-West Pacific distribution.

Table 2.1. Polyphyletic Mugilidae species in the molecular phylogenetic trees of Durand et al. (2012a,b).

Species	NL	Sp.	%DinterL COI	%DintraL COI	NSyn/L COI (a)	Gene Isol	Range
<i>Chelon dumerili</i>	2	M	6.6	[0-0.1]	5/11	na	Pa
<i>Crenimugil seheli</i>	3	P	[5.5-9.3]	[0.1-0.14]	8/4/11	na	S
<i>Dajaus monticola</i>	3	M	[7.4-14.6]	[0-0.2]	25/20/na	na	A/S
<i>Elochelone vaigiensis</i>	2	M	5.8	0	32/na	na	?
<i>Mugil cephalus</i>	14	P	[1-5.9]	[0-0.6]	3/0/3/5/2/2/0/1/0/1/1/1/12/3	na/Yes (b, c)	A/S
<i>Mugil curema</i>	4	P	[3.3-5.6]	[0.1-0.5]	7/4/5/5	Yes (d)	A/S
<i>Mugil rubrioculus</i>	2	M	5.5	na	na	na	A
<i>Osteomugil cunnesius</i>	3	P	[10.4-12.9]	[0-0.7]	10/na/na	na	A
<i>Planiliza alata</i>	2	P	13.1	[0-0.2]	1/8	na	A
<i>Planiliza macrolepis</i>	2	M	3.9	[0-0.11]	2/1	na	A
<i>Planiliza melinoptera</i>	2	P	13.7	0	3/na	na	S
<i>Planiliza tade</i>	2	P	14.3	na	na	na	?

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All lineages (41) are putative cryptic species considering the monophyly (M)/paraphyly (P) of the nominal species (Sp.), the ratio between the level of interlineage divergence (%DinterL) and the intralocus nucleotide diversity (%DintraL) estimated using the nucleotide polymorphism of the cytochrome oxidase I (COI) fragment, the number of synapomorphies per lineage (NSyn/L), the genetic isolation and the distribution range (Pa: parapatric, S: sympatric, A: allopatric). NL: number of lineage, na: not available. (a) Durand and Borsa (2015), (b) Shen et al. (2011), (c) Krüeck et al. (2013), (d) Durand et al. (2012a).

Dajaus Valenciennes, 1836, in Cuvier and Valenciennes, 1836

Type species. *Mugil monticola* Bancroft 1834. No types preserved.

Valenciennes in Cuvier and Valenciennes (1836) described the genus *Dajaus* for *Mugil monticola* present in the West Indies, which was later synonymized with *Agonostomus* by Günther (1861). However, paraphyly of the genus *Agonostomus* justifies the resurrection of the genus *Dajaus* (Durand et al. 2012b). *Dajaus* is the brother genus of *Agonostomus* and *Joturus* inside the Mugilinae subfamily (Xia et al. submitted, Fig. 2.1). No diagnostic morpho-anatomical traits were revealed (Xia et al. submitted, Fig. 2.2). Only one nominal species has been described, *Dajaus monticola*, but recent genetic investigations indicated the existence of three to four cryptic species (Durand et al. 2012a, McMahan et al. 2013, Table 2.1). The genus *Dajaus* occurs in rivers of the West Indies and Americas, from Florida to Venezuela and California to the Galapagos Islands (Thomson 1997).

Ellochelon Whitley, 1930

Type species. *Mugil vaigiensis* Quoy and Gaimard 1825 (holotype MNHN A-3641). Pulau Waigeo, Papua Barat province, Indonesia, western Pacific.

All molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with taxonomy based on morphological and anatomical traits (Eschmeyer and Fong 2014). The genus *Ellochelon* is the brother genus of *Plicomugil*, part of the Squalomugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). *Ellochelon* is supported by three diagnostic morpho-anatomical traits among genera of the Squalomugilini tribe, and one among genera of the Rhinomugilinae subfamily: interorbital shape flat (Xia et al. submitted). *Ellochelon* would be monotypic but there is some evidence of cryptic diversity that question species composition in this genus (see hereafter, Table 2.1). This genus has a wide Indo-West Pacific distribution, from Natal in South Africa to Tahiti (Thomson 1997).

Gracilimugil Whitley, 1941

Type species. *Mugil ramsayi* Macleay 1883 (syntypes: AMS IA.5944-46). Burdekin River, Queensland, Australia.

Most recent Mugilidae taxonomic revisions based on morpho-anatomical traits contest the findings of Whitley (1941) or Ghasemzadeh (1998), and assign *Mugil argenteus* (the senior synonym of *Mugil ramsayi*) to the genus *Chelon* (Senou 1988) or *Liza* (Thomson 1997, Harrison and Senou 1997, Kottelat 2013, Eschmeyer and Fong 2014). However, molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) clearly demonstrate that *Mugil argenteus* is an independent evolutionary lineage justifying validity of the genus *Gracilimugil* (Durand et al. 2012b). It is a monotypic genus, brother of *Aldrichetta*, within the Trachystomainsi tribe in the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). Eight diagnostic morpho-anatomical traits characterized *Gracilimugil* among genera of its tribe: adipose eyelid reaching the rim of eye, tendon flange 1/2–2/3 down maxilla shaft, pads over maxilla and the tendon to the mouth, tongue keeled, mouth gape horizontal or slightly oblique, two valves in pharyngobranchial organ, gills rakers very long (Xia et al. submitted, Fig. 2.2). This genus occurs in western Australia from Cardwell in Queensland to the Moor River (Thomson 1997).

Joturus Poey, 1860

Type species. *Joturus pichardi* Poey 1860 (holotype: MCZ 23886, possible type: USNM 132429). Río Almendares, near Havana, Cuba.

All molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with taxonomy based on morphological and anatomical traits (Eschmeyer and Fong 2014). The genus *Joturus* is the brother genus of *Dajaus* and *Agonostomus* within the Mugilinae subfamily (Fig. 2.1). It is supported by three diagnostic morpho-anatomical traits: upper lip recessed under snout, nine soft rays in the second dorsal fin, 11 soft rays in the anal fin (Xia et al. submitted, Fig. 2.2). This genus would be monotypic, but there is evidence of cryptic species in nominal species on both sides of the American continent, such as *Dajaus monticola* (Durand et al. 2012a, McMahan et al. 2012, Table 2.1). This genus occurs on both the Pacific and the Atlantic Coasts of the American continent, from Mexico to Panama, and in the Caribbean Sea (Thomson 1997).

Minimugil Senou, 1988

Type species. *Mugil cascasia* Hamilton 1822 (no types known). Rivers of northern Bengal.

Fowler (1939) created the genus *Sicamugil* for two small freshwater species *Mugil hamiltoni* (type species) and *Mugil cascasia*. While most recent revisions based on morpho-anatomical traits have

subscribed to this view (Thomson 1997, Eschmeyer and Fong 2014), Senou (1998) considered that the morpho-anatomical differences between these two species are greater than a congeneric level and created the genus *Minimugil*, with *Mugil cascasia* as type species. Molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with Senou's view because *Mugil cascasia* is phylogenetically closer to *Rhinomugil corsula* than to *Sicamugil hamiltoni*. It is the brother genus of *Rhinomugil*, part of the Rhinomugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). Among genera of the tribe, this genus is supported by two diagnostic morpho-anatomical traits: first dorsal fin origin nearer snout tip than to caudal base, height of the 2nd dorsal fin equal as the 1st one (Xia et al. submitted, Fig. 2.2). The only known species of this genus, *M. cascasia*, is distributed in the Ganges River and its tributaries (Thomson 1997).

Mugil Linnaeus, 1758

Type species. *Mugil cephalus* Linnaeus 1758 (possible syntypes: NRM 43, 44, 143). European sea, Europe.

All phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with taxonomy based on morphological and anatomical traits compiled by Eschmeyer and Fong (2014). The genus *Mugil* is the brother genus of *Chaenomugil* inside the Mugilinae subfamily (Xia et al. submitted, Fig. 2.1). It is supported by four diagnostic morpho-anatomical traits: nostrils nearer lip and eye than to each other, adipose tissue on face intruding over eye to pupil, distinct and long pectoral axillary scale, gill rakers long (Xia et al. submitted, Fig. 2.2). This genus comprises 13 nominal species: *M. bananensis*, *M. broussonetii*, *M. capurii*, *M. cephalus*, *M. curema*, *M. curvidens*, *M. hospes*, *M. incilis*, *M. liza*, *M. rubrioculus*, *M. setosus*, *M. thoburni*, *M. trichodon*. The species diversity of this genus is probably largely underestimated however, because cryptic species have been assumed for some species presenting large distribution ranges that encompass well known biogeographic barriers (see hereafter, Table 2.1). The genus *Mugil* has a worldwide distribution with the exception of Arctic and Antarctic seas (Thomson 1997).

Myxus Günther, 1861

Type species. *Myxus elongatus* Günther 1861 (syntypes: BMNH 1847.6.17.33 and 1847.10.22.16). Coast of Australia.

All phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) demonstrate that *Myxus elongatus*, the type species of the genus *Myxus*, has no close phylogenetic relationships with any other Mugilidae species, especially not to *Mugil capensis* and *Mugil petardi* that previously were assigned to the same genus (Thomson 1997, Harrison and Senou 1997). Consequently, *Myxus* would be a monotypic genus, brother of the genus *Neomyxus* inside the *Myxinae* subfamily (Xia et al. submitted, Fig. 2.1). This genus is supported by 14 diagnostic morpho-anatomical traits: maxima below mouth corner when mouth closed visible, preorbital front edge notched, preorbital filling space between lip and eye, posterior nostril not reaching above level of upper rim of eye, lower lip or its edge folded down absent, lip groove present, mouth corner reaching horizontal above lower rim of eye, vomer teeth present, palatine teeth present, seven-eight soft rays in the 2nd dorsal fin, caudal fin forked, height of the 1st dorsal fin equal to the 2nd dorsal fin, multicanalicate scale absent, wide sulcus in the pharyngobranchial organ (Xia et al. submitted, Fig. 2.2). The genus *Myxus* is restricted to temperate waters of Australia.

Neochelon Durand, Chen, Shen, Fu and Borsa, 2012

Type species. *Mugil falcipinnis* Valenciennes in Cuvier and Valenciennes 1836 (syntypes: MNHN A-3728, A-3729). Senegal.

While *Mugil falcipinnis* has been considered as part of the genus *Liza* or *Chelon* in all taxonomic revisions based on morpho-anatomical traits (Harrison and Howes 1991, Albaret 1992, Thomson 1997), its unique

placement in the Mugilidae phylogenetic tree (Durand et al. 2012a) lead Durand et al. (2012b) to create the genus *Neochelon*. In the phylogenetic tree that combines mitochondrial and nuclear gene sequences (Fig. 2.1), *Neochelon* is the most divergent genus among all genera of the Cheloninae subfamily (Xia et al. submitted). It is supported by two diagnostic morpho-anatomical traits: 11 soft rays in the anal fin, scales with a membranous, digitated hind margin (Xia et al. submitted, Fig. 2.2). *Neochelon falcipinnis* the unique species of the genus *Neochelon*, occurs in West Africa from Saint-Louis in northern Senegal to Congo (Thomson 1997).

Neomyxus Steindachner, 1878

Type species. *Myxus (Neomyxus) sclateri* Steindachner 1878 (syntypes: NMW 67168, 77884, 82505). Gilbert Islands and Hawaiian Islands.

All phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) are in agreement with the taxonomy based on morphological and anatomical traits (Eschmeyer and Fong 2014). *Neomyxus* is the brother genus of *Myxus*, within the *Myxinae* subfamily (Xia et al. submitted, Fig. 2.1). This genus is supported by 14 diagnostic morpho-anatomical traits: maxima below the mouth corner when mouth closed not visible, preorbital front edge not notched, preorbital not filling space between lip and eye, posterior nostril reaching above level of upper rim of eye, lower lip or its edge folded down present, lip groove absent, mouth corner reaching horizontal at or below lower rim of eye, vomerine teeth absent, palatine teeth absent, nine soft rays in the 2nd dorsal fin, caudal fin emarginated, height of the 1st dorsal fin lower than the 2nd dorsal fin, multicanalicate scale present, narrow sulcus in the pharyngobranchial organ (Xia et al. submitted, Fig. 2.2). The only representative of this genus, *N. leuciscus*, occurs around islands of the central Pacific, from the southern Japanese and Hawaiian islands to Samoa (Thomson 1997).

Oedalechilus Fowler, 1903

Type species. *Mugil labeo* Cuvier 1829 (lectotype: MNHN A-3606, Paralectotypes: MNHN A-3607, A-4654). Mediterranean Sea.

All phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) stress the paraphyly of *Oedalechilus*, when *Mugil labeo* and *Mugil labiosus* are assigned to the same genus, as proposed by several authors on the basis of morphological and anatomical similarities (Senou 1988, Thomson 1997, Senou 2002). In fact, the type species *O. labeo* has no close phylogenetic relationships with any species within a clade comprising various genera, including *Chelon* (Fig. 2.1). Consequently, *Oedalechilus* is a monotypic genus belonging to the Cheloninae subfamily (Xia et al. submitted). This genus is supported by four diagnostic morpho-anatomical traits: posterior nostril reaching above level of upper rim of the eye, lower lip or its edge folded down, a single pair of shelf-like fold inside the mouth corner, labial teeth absent (Xia et al. submitted, Fig. 2.2). The only representative of this genus, *O. labeo*, occurs in the western Mediterranean Sea and the Azores archipelago (Thomson 1997).

Osteomugil Lüther, 1977

Type species. *Mugil cunnesius* Valenciennes 1836 (syntypes: MNHN A-4636 Moluccas, A-3701-02 Mumbai, A-3726-27 Malabar, B-2678 [ex A-3702], B-2629 [ex A-3701], 1992-0561 [ex A-3727]). Coromandel coast, India; Molucca Islands, Indonesia; Mumbai, India.

The genus *Osteomugil* was created by Lüther (1977) on the basis of some osteological characters that differentiate *Mugil cunnesius* (the type species) and possibly *Mugil perusii* and *Mugil engeli* from other species belonging to *Liza* (synonymized here with *Chelon*), *Valamugil* (synonymized here with *Crenimugil*)

and *Ellochelon*. Phylogenetic reconstructions (Durand et al. 2012a, Xia et al. submitted) based on various gene sequences demonstrated that all *Osteomugil* species belong to the same clade, leading Durand et al. (2012b) to resurrect this genus, which had been synonymized with *Valamugil* by Thomson (1997). *Osteomugil* is the brother genus of *Crenimugil* sensu Durand et al. (2012b), part of the Crenimugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). Within its subfamily, *Osteomugil* is characterized by a combination of morpho-anatomical characters: the two synapomorphies of the Crenimugilini tribe and the adipose eyelid reaching iris of the eye (Xia et al. submitted, Fig. 2.2). The *Osteomugil* genus consists of five nominal species: *O. cunnesius*, *O. engeli*, *O. robustus*, *O. speigleiri*, and *O. perusii*. However, species diversity in the genus is probably underestimated (Table 2.1). It is widespread across the Indo-Pacific, from Africa to the Marquesas and Tuamotu Islands, north to southern Japan.

Parachelon Durand, Chen, Shen, Fu and Borsa, 2012

Type species. *Mugil grandisquamis* Valenciennes in Cuvier and Valenciennes 1836 (lectotype: MNHN A-3743, paralectotypes: MNHN A-3744, A-3745). Gorée, Senegal.

In all recent taxonomic reviews based on morpho-anatomical traits, *Mugil grandisquamis* is assigned to the genus *Liza* or *Chelon* (Albaret 1992, Senou 1988, Thomson 1997). However, its unique placement in the mitochondrial phylogenetic tree (Durand et al. 2012a) justifies the creation of the genus *Parachelon* (Durand et al. 2012b). Xia et al. (submitted, Fig. 2.1) confirmed this placement. Plotting 68 morpho-anatomical traits on the molecular tree did not however, reveal any diagnostic traits (Xia et al. submitted). Nevertheless, Harrison and Howes (1991) noticed that the pharyngobranchial organ morphology of *L. grandisquamis* is more similar to species from other genera *Crenimugil* (*C. seheli*), *Ellochelon* (*E. vaigiensis*), and *Paramugil* (*P. parmatus*) than to any other *Liza* species (*Chelon* and *Planiliza*). *Parachelon* is the brother genus of *Chelon* and *Planiliza* within the Cheloninae subfamily (Xia et al. submitted, Fig. 2.1). The only known species of the genus, *Parachelon grandisquamis* occurs in West Africa, from Senegal to Nigeria (Thomson 1997).

Planiliza Whitley, 1945

Type species. *Moolgarda (Planiliza) ordensis* Whitley 1945. Type by original designation.

All Indo-Pacific species previously assigned to *Chelon*, *Liza* and its synonym *Planiliza* genera constituted a strongly supported clade in molecular phylogenies (Durand et al. 2012a, Xia et al. submitted, Fig. 2.1). Durand et al. (2012b) resurrected the genus *Planiliza* for species in this clade because type species of genera *Liza* and *Chelon* belong to another clade. *Planiliza* is the brother genus of genera *Chelon* and *Parachelon* within the Cheloninae subfamily (Xia et al. submitted). Xia et al. (submitted) did not identify diagnostic traits among 68 morpho-anatomical traits (Fig. 2.2), but a distribution range limited to the Indo-Pacific Ocean clearly distinguishes them from their closest relatives (*Chelon* and *Parachelon*) that are present in the Atlantic, Mediterranean and temperate waters off South Africa. This genus is one of the most diversified of the Mugilidae and further phylogenetic investigation is needed to determine species diversity. The phylogenetic tree provided by Durand et al. (2012a) included several undetermined or paraphyletic species (see hereafter, Table 2.1). Based on molecular evidence, the following nominal species belong to this genus: *P. abu*, *P. affinis* (synonymized with *P. lauvergnii* in Eschmeyer and Fong 2014's revision), *P. alata*, *P. carinata*, *P. haematocheila*, *P. klunzingeri*, *P. melinoptera*, *P. subviridis*, *P. macrolepis*, *P. ordensis*, *P. tade*. The genus is widely distributed in the Indo-Pacific from the Red Sea to Oceania. It has been observed recently in the Mediterranean Sea (*P. carinata*) and in the Black Sea (*P. haematocheila*) due, respectively, to migration through the Suez Canal or to introduction for commercial purposes.

Plicomugil Schultz, 1953

Type species. *Mugil labiosus* Valenciennes 1836 (syntypes: MNHN A-3616, A-3617). Red Sea; Mumbai, India.

The genus *Plicomugil* was created by Schultz (1953) who considered that *Mugil labiosus* shows outstanding development of the mouthparts that does not overlap those of other species, especially with *Mugil labeo* that had been considered congeneric. This genus was however, constantly synonymized with *Oedalechilus* in all later taxonomic revisions (Thomson 1997, Senou 1998, Ghasemzadeh 1998, Senou 2002, Eschmeyer and Fong 2014) despite some contrasting anatomical evidence (Harrison and Howes 1991). In molecular phylogenetic reconstructions (Durand et al. 2012a, Xia et al. submitted) *M. labiosus* shows no close phylogenetic relationships with *O. labeo*, which justified the resurrection of *Plicomugil* (Durand et al. 2012b). It is the brother genus of *Ellochelon* part of the Squalomugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). Among genera of the tribe, it is supported by 13 diagnostic morpho-anatomical traits; one still diagnostic when considering all genera of the subfamily: four pairs of shelf-like folds inside the mouth corner (Xia et al. submitted, Fig. 2.2). This monotypic genus occurs in the Red Sea and Indo-Pacific from East Africa to the Marshall Islands and from southern Japan to Queensland, Australia (Eschmeyer and Fong 2014).

Pseudomyxus Durand, Chen, Shen, Fu and Borsa, 2012

Type species. *Mugil capensis* Valenciennes in Cuvier and Valenciennes 1836 (syntypes: MNHN A-4643, A-4700). Cape of Good Hope, South Africa.

In all taxonomic revisions based on morpho-anatomical traits, *Mugil capensis* has been considered part of the genus *Myxus* (Smith and Smith 1986, Heemstra and Heemstra 2004, Thomson 1997). Molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) demonstrated however, that this species has no close phylogenetic relationships with *Myxus elongatus* and, among the subfamily Cheloninae *sensu* Xia et al. (submitted), is one of the most divergent species (Fig. 2.1). On the basis of the molecular phylogeny, Durand et al. (2012b) created the genus *Pseudomyxus*. This genus is also supported by seven diagnostic morpho-anatomical traits: adipose eyelid absent, tendon flange < 1/2 way down the maxilla shaft, pads over the lower end of the maxilla absent, or only over the tendon to the mouth, lip groove present, mouth gape moderately oblique, nine soft rays in the second dorsal fin, short length of mucus canals on scales (Thomson 1997, Xia et al. submitted, Fig. 2.2). The genus *Pseudomyxus* is monotypic and occurs in South Africa (Thomson 1997).

Rhinomugil Gill, 1863

Type species. *Mugil corsula* Hamilton 1822. No types known.

In all taxonomic revisions based on morpho-anatomical traits, the genus *Rhinomugil* comprises two species: *Mugil corsula* (the type species) and *Mugil nasutus* (Schultz 1946, Thomson 1997, Senou 1998, Eschmeyer 2014). Recent molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) demonstrated however, that these two species do not belong to the same genus or even the same tribe (Xia et al. submitted, Fig. 2.1). Because the type species of *Rhinomugil* is *Mugil corsula*, only this species is maintained in this genus which is brother of *Minimugil*, part of the Rhinomugilini tribe within the Rhinomugilinae subfamily (Fig. 2.1). Among genera of the tribe, the *Rhinomugil* genus is supported by 15 diagnostic morpho-anatomical traits: adipose eyelid extending over iris, preorbital not filling space between lip and eye, interorbital concave, eyes raised above dorsal contour of head, opercular spin absent, upper lip recessed under snout, mouth gape very slightly oblique, mouth corner at level below lower rim of eye, mouth corner reaching vertical at or behind posterior nostril, tongue teeth absent, caudal fin slightly forked, second dorsal fin origin at vertical $\geq 2/3$ along anal fin base, pectoral fin past tip of pelvic spine

when laid back, axillary scale short, large or moderate size of denticulate area in the pharyngobranchial organ (Thomson 1997, Xia et al. submitted, Fig. 2.2). This genus occurs in freshwaters of the Indian subcontinent (Thomson 1997).

Squalomugil Ogilby, 1908

Type species. *Mugil nasutus* De Vis 1883 (holotype: QM I.120, non-types: AMS I.12693). Cardwell, Rockingham Bay, Queensland, Australia.

Ogilby (1908) created the *Squalomugil* genus, apparently in ignorance of Gill's work (Thomson 1997). No subsequent taxonomic revision considered this genus as valid (Schultz 1946, Thomson 1997, Senou 1998, Eschmeyer and Fong 2014), except Taylor (1964) on the basis of the different position of the nostrils between *Mugil nasutus* and *Mugil corsula*. As mentioned in the *Rhinomugil* section however, all molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) have justified the validity of *Squalomugil*, being closer to the type species of genera such as *Ellochelon* and *Plicomugil* than to the type species of *Rhinomugil* (Fig. 2.1). It forms with its brothers genera the Squalomugilini tribe inside the Rhinomugilinae subfamily (Xia et al. submitted). Among genera of its tribe, it is supported by 18 diagnostic morpho-anatomical traits: maxilla below the mouth corner when mouth closed was not visible, nostrils farther to each other than to eye or lip, adipose eyelid extending over iris, no scale free area on top of the head, pads over the lower end of the maxilla and over the tendon to the mouth absent or only over the tendon to the mouth, preorbital not filling space between lip and eye, interorbital concave, eyes raised above dorsal contour of head, lip groove present, upper lip recessed under snout, mouth corner at level below lower rim of eye, no vomer, endopterygoid, palatine and tongue teeth, upper insertion of pectoral fin at or below mid-eye level, axillary scale reaching $< \frac{1}{2}$ along pelvic spine, no multicanalicate scale (Thomson 1997, Xia et al. submitted, Fig. 2.2). The only known species of this genus, *S. nasutus*, occurs in tropical Australia and the southern shores of New Guinea (Thomson 1997).

Sicamugil Fowler, 1939

Type species. *Mugil hamiltoni* Day 1869 (syntypes or Day specimens: AMS B.7993; BMNH 1889.2.1.3724-3725; MCZ 17525; NMW 67653; ZSI F11401, A.355, B.150). Irrawaddy River, Pegu, and other rivers of Myanmar.

Molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted) have demonstrated that the genus *Sicamugil* is paraphyletic when *M. cascasia* is considered congeneric. For this reason, Durand et al. (2012b) maintained *Sicamugil* for *S. hamiltoni*, the type species of the genus. The *Sicamugil* genus is part of the Rhinomugilini tribe within the Rhinomugilinae subfamily (Xia et al. submitted, Fig. 2.1). It is supported by one diagnostic morpho-anatomical traits: the axillary scale does not reach the base of the spine IV (Xia et al. submitted, Fig. 2.2). The only known species of this genus, *S. hamiltoni*, occurs in rivers of Myanmar (Thomson 1997).

Trachystoma Ogilby, 1888

Type species. *Trachystoma multidentis* Ogilby 1888 (no types known). Brackish water at Keruah River mouth, Port Stephens, Australia.

Due to the close external morphological similarity of *Trachystoma multidentis* (junior synonym of *Mugil petardi*) to *Myxus elongates*, the type species of the genus *Myxus*, some taxonomical revisions have considered *Trachystoma* as a junior synonym of *Myxus* (Thomson 1997, Harrison and Senou 1997). In molecular phylogenetic reconstructions (Durand et al. 2012a,b, Xia et al. submitted), the species *Mugil petardi* formed a distinct and unique clade, which confirmed the peculiar systematic status of the monotypic genus *Trachystoma*. It is the brother genus of two genera, *Aldrichetta* and *Gracilimugil*, which occur in the same biogeographic area, within the Trachystomaini tribe of the Rhinomugilinae subfamily

(Xia et al. submitted, Fig. 2.1). Among genera of the tribe, the genus *Trachystoma* is supported by one diagnostic morpho-anatomical traits: in the first dorsal fin, spine I equal or longer than spine II (Xia et al. submitted, Fig. 2.2). *T. petardi*, the only species in the genus, inhabits the rivers of eastern Australia, from Queensland to New South Wales (Thomson 1997).

Other Genera

In this chapter, the validity of *Paracrenimugil* Senou 1988 and *Paramugil* Ghasemzadeh 1998 has not been evaluated because there are no molecular phylogenetic reconstructions available that included specimens of these genera. Senou (1988) created the monotypic genus *Paracrenimugil* with regard to a phylogenetic reconstruction based on 46 morphological characters. These placed *Mugil heterocheilos* Bleeker 1855 basal in a clade that included two subclades corresponding to the genera *Crenimugil* and *Osteomugil* (Durand et al. 2012b). Concerning the *Paramugil* genus, it was created by Ghasemzadeh (1998) on the basis of 18 diagnostic morphological and osteological differences that distinguished *Mugil parmatus* Cantator 1849 (type species) and *Mugil georgii* Ogilby 1897 from other species belonging to *Liza*, *Valamugil* and/or *Mugil* genera. Before Ghasemzadeh (1998), Senou (1988) had already suggested that *Mugil parmatus* Cantator 1849 belonged to a specific genus and had created the monotypic genus *Pseudoliza*. Despite this morpho-anatomical evidence, Durand et al. (2012b) synonymized *Paramugil* with *Planiliza* on the basis of the molecular phylogenetic tree of Durand et al. (2012a). However, Ghasemzadeh recently studied the morphology of the specimen MNHN-IC-2011-0212 identified as *Liza parmata* in the study of Durand et al. (2012a) and he concluded that it was misidentified, as its morpho-anatomical and meristic traits corresponded to *Planiliza melinoptera*. Consequently, new specimens of *Mugil parmatus* are needed to determine the phylogenetic relationships of this species within the Mugilidae.

Species

Numerous species have been described over the last two centuries. According to Thomson (1954) however, mugilid species diversity has probably been much overestimated because most of the earlier taxonomic work relied on the examination of specimens collected locally, without comparing these to morphologically similar species described elsewhere. In his last systematic revision, Thomson (1997) accepted only 62 species as valid among the existing 280 nominal species. Delimiting species boundaries in the Mugilidae is tricky because morpho-anatomical traits present ranges of variation that frequently overlap between taxa. In this context, DNA-based approaches can be used to identify species within taxa that have been overlooked or that present low levels of morpho-anatomical variation (Petit and Excoffier 2009, Zou et al. 2011, Kekkonen and Hebert 2014). Integration of criteria inferred from phylogeny, phylogeography and population genetics studies could produce primary species hypotheses that can be further tested, using morphological, ecological, behavioural, and geographic criteria. Among DNA-based criteria, monophyly, the presence of fixed mutations (character-based DNA barcoding), the geographic distribution of genetic diversity, and reproductive isolation, are species properties in various species concepts (de Queiroz 2007). Despite their varied perspectives and occasional incompatibilities, according to de Queiroz (2007), “a unified species concept can be achieved by treating existence as a separately evolving metapopulation lineage as the only necessary property of species” and other criteria such as different lines of evidence (operational criteria) relevant to assessing lineage separation. Considering these operational criteria, the species diversity of the Mugilidae is probably much greater than assumed by Thomson (1997). Using a sample of 257 individuals from 53 recognized species, Durand et al. (2012a,b) highlighted 91 lineages or Operational Taxonomic Units (OTUs) in the Mugilidae phylogenetic tree. Seven of these OTUs were in samples of undescribed species (because the morpho-anatomical description was either not available or did not match any species description). Among recognized species, 12 were polyphyletic and harboured from two to 14 lineages with levels of divergence that greatly exceed the average intraspecific differentiation or distance (D, Kimura’s two-parameter model; Kimura 1980), which is estimated with the COI marker to be 0.35% in fishes (Ward et al. 2009, Table 2.1). Although some authors contest the level of divergence as a species criterion (Ferguson 2002), up to seven of the polyphyletic species were paraphyletic, which is

the first line of evidence for the presence of cryptic species in Mugilidae. When paraphyly is not proven, there is some evidence of reproductive isolation, such as demonstrated for some sympatric lineages within the nominal species *Mugil cephalus* (Shen et al. 2011, Krüeck et al. 2013). Similarly, among four lineages observed in *M. curema*, two are in allopatry, separated by well known biogeographic barriers (the American continent and the Atlantic Ocean) while those potentially in sympatry present two different cytotypes ($2n = 24$ and $2n = 28$) which probably prevent interbreeding (Durand et al. 2012a).

To conclude, there is increasing molecular evidence that the species diversity of the Mugilidae is greatly underestimated (Durand and Borsa 2015). Morphometry and anatomy are sometimes useful to describe mugilid diversity, as for *Mugil rubrioculus* in 2007 (Harrison et al. 2007), but there is no doubt that molecular approaches are very valuable, while not the only possible approaches, in providing rapid advances in knowledge of this family. In this context, DNA barcoding programmes such as FISHBOL (<http://www.fishbol.org>) represent an excellent opportunity to reveal putative cryptic species. However, it would first be necessary to evaluate the sequence variability of the *COI* fragment used in barcoding programmes to know if it is able to identify putative cryptic species highlighted in this present study.

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CHAPTER 3

Biogeography and Distribution of Mugilidae in the Americas

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American Biogeographic Shelf Regions and Provinces

The American continent stretches for about 14000 km from north to south, spanning over 127° of latitude (72° N to 55° S) and covering approximately 42.5 million km² (Kohn and Cohen 1998). The continent is bordered by the Atlantic Ocean on the east and the Pacific on the west. The latitudinal range confers important biogeographical and ecological characteristics to this landmass. The most obvious is the freshwater outflow from the Amazon River to the Atlantic that apparently acts as a biogeographical barrier separating the fish fauna of Brazil and the Caribbean (Briggs 1995). According to Briggs (1995), the distribution patterns of aquatic species in local situations may be affected by factors such as food, shelter, salinity and dissolved oxygen, but on a global or oceanic scale, temperature primarily controls their distribution. The widespread patterns demonstrated by many species indicate that the surface of the ocean is subdivided into four zones: the Tropical Zone (TR), the Warm-Temperate Zone (W-T), the Cold-Temperate Zone (C-T), and the Cold or Polar Zone (C), each with their respective regions and zoogeographical provinces (Briggs 1995). However, the upsurge of more information on phylogeography, palaeontological research, earth movements and sea level changes in the last 20 years required a new arrangement of regions and provinces (Briggs and Bowen 2012). Moreover, the provinces proposed by Briggs (1995) have recently been subdivided into ecoregions to address the appropriate scale of conservation efforts (Spalding et al. 2007). Biogeographic classifications are essential for developing ecologically representative systems of protected areas, as required by international agreements for conservation and regional fisheries management. The biogeographic classification proposed by Spalding et al. (2007) focuses on coastal and shelf waters, combining benthic and shelf-dependent pelagic biotas, representing waters where most of the marine biodiversity is confined, human attention is higher, and where there is often a complex synergy of threats—far greater than in offshore waters. According to the biogeographic division of Spalding et al. (2007), the American continent contains five large realms (Temperate northern Atlantic, Temperate northern Pacific, Tropical Atlantic, Tropical eastern Pacific and Temperate South America), each with its respective provinces and ecoregions (Fig. 3.1, Table 3.1).

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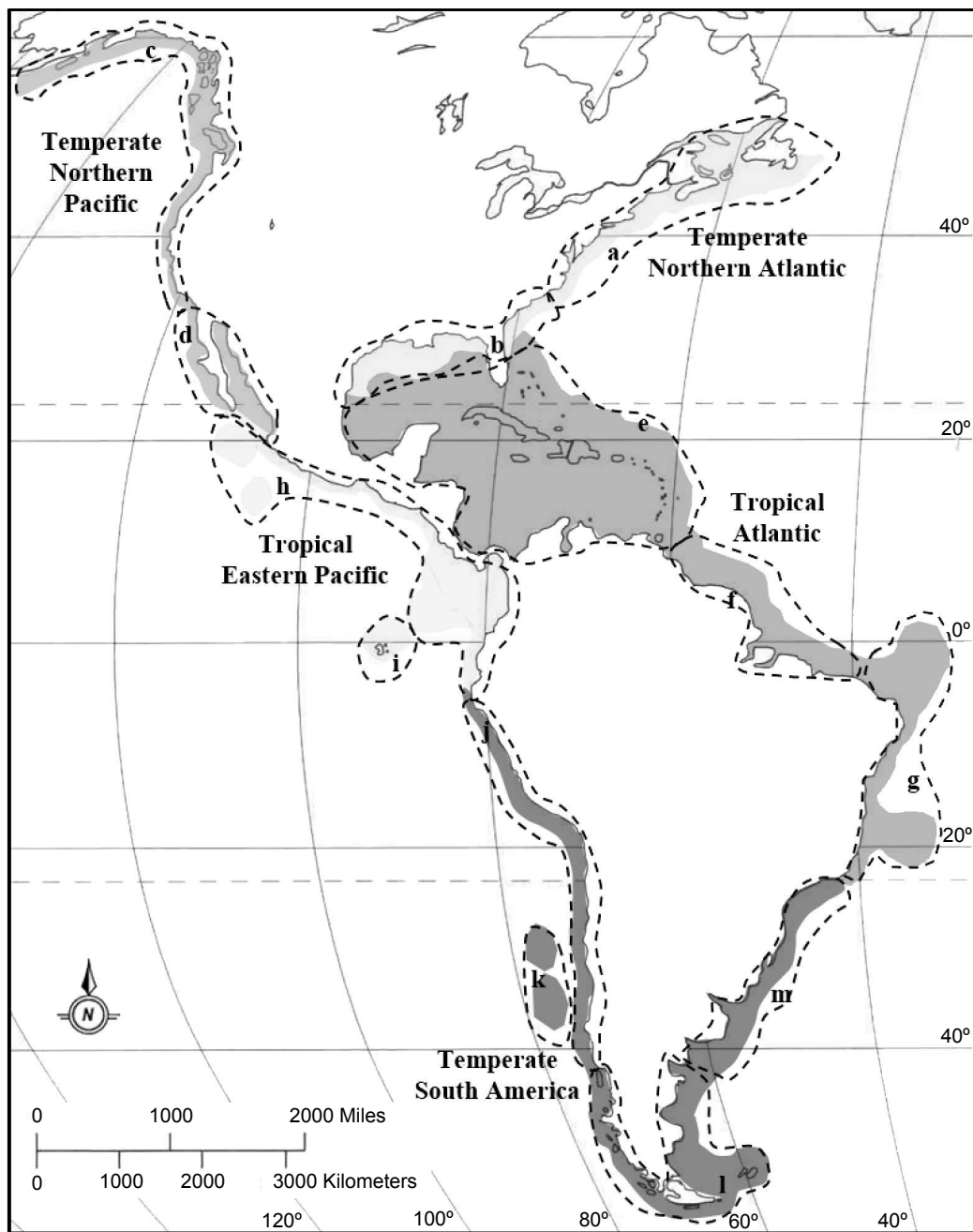


Figure 3.1. Marine realms and provinces in the America continent (North, Central and South). The realms are indicated in different shades and provinces in letters delimited by draw lines: (a) Cold Temperate Northwest Atlantic; (b) Warm Temperate Northwest Atlantic; (c) Cold Temperate Northeast Pacific; (d) Warm Temperate Northeast Pacific; (e) Tropical Northwestern Atlantic; (f) North Brazil Shelf; (g) Tropical Southwestern Atlantic; (h) Tropical East Pacific; (i) Galapagos; (j) Warm Temperate Southeastern Pacific; (k) Juan Fernández and Desventuradas; (l) Megallanic; (m) Warm Temperate Southwestern Atlantic.