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PAST AND FUTURE OF CYTOGENETICS OF MUGILIDAE: AN UPDATED OVERVIEW

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ABSTRACT: Mugilidae (Teleostei) include over 70 species worldwide, and approximately 25% of them have been cytogenetically analyzed. Although a review of Mugilidae genetics was recently published, new data have provided a different perspective on the cytotaxonomic relationships of this group and generated a revision of the chromosomal evolution of their family. Most mugilid species possess the conservative 48-uniarmed chromosome karyotype, with some differences hinging on the presence or absence of short arms on a sole subtelocentric chromosome pair, thus allowing the identification of two distinct cytotypes, namely A and B, respectively. Differences in constitutive heterochromatin and in the location of genes 18S and 5S rRNA can be found within and between these two cytotypes. A recent analysis of the karyotype of *Agonostomus monticola*, the family's most basal species, ascertained that it possesses the B cytotype; and offers the opportunity to both reconsider relations between the two cytotypes and infer the direction of chromosomal changes during the evolution of the group, suggesting that cytotype B could be closer to the ancestral karyotype. *Mugil curema* is an exception to this scenario, having two different cytotypes (C1 and C2) in terms of number of chromosomes, NOR location, and heterochromatin distribution, though both are mainly or exclusively constituted by biarmed chromosomes. However, neither of the cytotypes (A or B) currently described in the family can be identified as being closer to the ancestral karyotype that underwent the Robertsonian fusion observed in the two C cytotypes; nor is it possible to infer a direct cytotaxonomic relationship between cytotypes C1 and C2. The cytogenetic features of the family entail a great opportunity to carry out cytotaxonomic and phylogenetic studies as well as structural, evolutionary, and functional analyses of the genome, *i.e.*, a cytogenomic approach. This entails the isolation and cloning of additional satellite DNA families and the production of specific painting probes to allow for whole chromosome painting, whose distribution in the karyotypes of different mugilid species will allow the investigation of inter-specific homologies and structural changes leading to mullet chromosomal complement divergence.

Key words: Mullets, karyotype divergence, evolution.

RESUMEN**:** La familia Mugilidae (Teleostei) incluye más de 70 especies distribuidas en todo el mundo y aproximadamente 25% han sido estudiadas citogenéticamente. Aunque recientemente fue publicada una revisión de la genética de la familia, datos actuales han proporcionado una perspectiva distinta de sus relaciones citotaxonómicas, lo que ha generado una revisión de la evolución cromosómica en el grupo. La mayoría de las especies de mugílidos poseen un cariotipo conservado, constituido por 48 cromosomas acrocéntricos, con diferencias en la presencia o ausencia de brazos cortos en un único par subtelocéntrico, lo que permite identificar dos citotipos, A y B, respectivamente. Diferencias en la composición de la heterocromatina constitutiva y en la localización de los genes 18S-rRNA y 5S-rRNA pueden ser encontradas en y entre estos dos citotipos. Un análisis reciente del cariotipo de *Agonostomus monticola*, especie más basal de la familia, reveló que posee el citotipo B, ofreciendo la oportunidad tanto de reconsiderar las relaciones entre los dos citotipos, como de inferir la dirección de los cambios cromosómicos ocurridos durante la evolución del grupo, y ha permitido sugerir que el citotipo B podría ser el más cercano al cariotipo ancestral. *Mugil curema* es una excepción dentro de este escenario, con dos citotipos (C1 y C2) constituidos principal o exclusivamente por elementos de dos brazos y que difieren en el número de cromosomas, localización de las NORs, y distribución de la heterocromatina constitutiva. Sin embargo, ninguno de los citotipos descritos (A o B) puede ser identificado como el más cercano al cariotipo ancestral que sufrió la fusión Robertsoniana observada en los dos citotipos C; ni tampoco es posible deducir una relación citotaxonómica directa entre los citotipos C1 y C2. Los detalles de las características citogenéticas de la familia brindan la posibilidad de realizar estudios citotaxonómicos y filogenéticos, así como también el análisis estructural, evolutivo y funcional del genoma, en una aproximación citogenómica. Esto requiere del aislamiento y clonación de familias adicionales de DNA satélite y de la producción de sondas específicas para emplear la técnica de *Whole Chromosome Painting* (pintado total del cromosoma), cuya distribución en los cariotipos de diversas especies del grupo permitirá investigar homologías interespecíficas y cambios estructurales que han conducido a la divergencia del complemento cromosómico de los mugílidos.

Palabras clave: Lisas, divergencia cariotípica, evolución.

BACKGROUND

Notwithstanding the recent publication of a Mugilidae cytogenetics review (SOLA *et al.* 2007), it is useful to make a re-visitation of the chromosomal evolution in the family on account of both published (NIRCHIO *et al.* 2007, 2008) and unpublished new data obtained on additional mullet species, a development that sheds new light on the cytotaxonomic relationship previously inferred for the Mugilidae species.

The systematic position of the family is quite complex and controversial. Indeed, up to 1958 the family was considered to be a representative of a distinct order, Mugiliformes (BERTIN & ARAMBOURG 1958); thereafter, and up to 1968, it was placed in a suborder of Perciformes (GOSLINE 1968). At present, the family is back in the order of Mugiliformes (THOMSON 1997; NELSON 2006) as its sole representative. Also, numerous systematic revisions have been carried out within the family at both the generic and specific level, due to the considerable morphological conservativeness of mullets. In addition to this, the interspecific differences of meristic and morphometric characters are often of the same extent of the intraspecific ones, and this also contributes to the emergence of numerous taxonomic and nomenclatural problems. The most recent revisions (THOMSON 1997; NELSON 2006) account for a number of valid species ranging from 62 to 72, grouped in 14 to 17 genera, distributed throughout all the temperate and tropical regions of the world. Most of the species inhabit coastal water and accomplish trophic migrations in brackish and, occasionally, freshwater environments as they are eurytherm and euryhaline.

Among the characters that differ from the morphological ones, the cytogenetic features may provide important insight into systematics. The so far published cytogenetic studies cover a total number of at least 17 species (grouped in seven genera), probably more, given that the karyological data have probably disclosed the existence of a *M. curema* species complex (NIRCHIO *et al.* 2005a). Cytogenetic data mainly refer to species sampled from Mediterranean (six species) or Caribbean and South American Atlantic (seven species) areas. Although the studied species approximately represent only 25% of living Mugilidae, the available cytogenetic data have already disclosed several really interesting issues which foster karyological studies on species of Mugilidae yet to be described.

Cytogenetic data published up to 2000 (reviewed in SOLA *et al.* 2007) indicated a high karyological conservativeness in the family. Indeed, 13 out of the 14 species studied until then show the 48 uniarmed karyotype proposed by OHNO (1974) as the karyotype of the ancestor of all Teleostei and more recently considered as restricted only to the ancestor of Clupeomorpha and Euteleostei by BRUM & GALETTI (1997). Whatever, this is certainly to be considered a conservative karyotype as it is displayed by a high number of un-related species. There already was, however, one notable exception, constituted by *Mugil curema*, as specimens from Louisiana (LE GRANDE & FITZSIMONS 1976) were found to have a karyotype mainly composed by biarmed chromosomes, with a diploid number of 28 and a conserved fundamental number (FN) of 48. Obviously, the authors interpreted this karyotype as a result of extensive Robertsonian fusions from an all uniarmed chromosome complement. Interestingly, more than 20 years later, specimens of *M. curema* from Isla de Margarita (NIRCHIO & CEQUEA 1998) have been found with 2n=24 and an exclusively biarmed karyotype.

CURRENTLY

The present state of the art of the cytogenetic knowledge in Mugilidae reflects the fact that after 2000, studies (reviewed in SOLA *et al.* 2007) were carried out by the application of differential staining techniques and fluorescence *in situ* hybridization (FISH) with several types of DNA probes, and that the investigations were extended to additional samples and species of mullets from Central America. Moreover, the latter studies integrated cytogenetic and morphological data.

Specifically talking about the species with the conservative 48 uniarmed chromosomes karyotype, actually two cytotypes (Fig. 1) can be identified among them. Indeed, there is a group of species which has only acrocentric chromosomes, *i.e.*, all chromosomes with a terminal centromere (cytotype A); and there is a second group of species which, among the acrocentric chromosomes, has one pair of subtelocentric chromosomes, *i.e.*, one pair of chromosomes with short arms (cytotype B). After the application of differential staining techniques and FISH, both cytotypes were found to be differentiated by finer cytogenetic features, such as the different location of genes for 18S rRNA and 5S rRNA and for the composition of the constitutive heterochromatin.

In more detail, cytotype A, with 48 acrocentric chromosomes, is displayed by ten species belonging to four genera from all over the world (Fig.1, references in SOLA *et al.* 2007). *M. cephalus*, from the Mediterranean, and *M. liza*, from Venezuela, have been investigated with all the above mentioned staining techniques and show an overlapping karyotype for the investigated cytogenetic features, as summarized in the idiograms of Fig. 1. All the techniques (silver- and Chromomycin A_3-staining, FISH with an 18S rDNA probe) generally used to investigate the location of major ribosomal genes were consistent in identifying only one chromosome pair to bear the Nucleolus Organizer Regions (NORs). Thus, in both species NORs are located in the terminal region of the largest chromosome pair, number 1. Similarly, in both species, FISH with a 5S rDNA probe provides fluorescent signals in an interstitial position of the smallest chromosome pair, number 24. A similar location for NORs was suggested by Ag-staining in *M. platanus* and *Rhinomugil corsula*.

Cytotype A, with the major (and minor) ribosomal gene locations observed in *M. liza* and *M. cephalus*, has been so far regarded as plesiomorphic in any cytotaxonomic consideration of the family (SOLA *et al.* 2007). In fact, it has to be emphasized that cytotype A is shared by all the *Mugil* species investigated (with the exception of *M. curema*) and this genus is phylogenetically more basal (THOMSON 1997) compared to the other genera (*Rhinomugil*, *Valamugil*, *Liza*, *Chelon*, *Oedalechilus*) karyologically studied until the early 2000s.

Under this perspective, *M. trichodon* was the first species to be described (NIRCHIO *et al.* 2005b) with an interstitial NOR location on a medium-sized chromosome, location which was a novelty in the genus and in the family, in general. This same species has been recently investigated for 5S rDNA, and these preliminary and still unpublished data suggest the presence of two different chromosomal locations for the minor ribosomal genes, both in heterozygotic condition in the only analyzed specimen (Fig. 1). Thus, the location of major and minor ribosomal genes in *M. trichodon* suggests their derived position and the occurrence of chromosome rearrangements.

Shortly thereafter (NIRCHIO *et al.* 2007), a second species from Isla de Margarita, *Mugil rubrioculus* (HARRISON *et al.* 2007), formerly *M. gaimardianus*, was found with interstitial NORs located on a different chromosome pair from that in which NORs are located in *M. trichodon*. Unpublished data are available on the 5S rDNA location in this species, the minor ribosomal genes being shown once again on a chromosome pair classified as number 13, different from the one observed in M. *trichodon*, *M cephalus*, and *M. liza*, as well as in any other species of the family (Fig. 1).

Thus, comparing the idiograms (Fig. 1) of *M. trichodon* and *M. rubrioculus* to the one of *M. cephalus* and *M. liza*, supposed to be the closest to the ancestral karyotype, it is hard to figure out their cytotaxonomic relationships; and several chromosomal rearrangements must be invoked to explain the different location of these markers, weakening, therefore, the original assumption of a high karyological conservativeness in Mugilidae.

As far as the second group of species with 46 acrocentrics and two subtelocentrics, i.e., with cytotype B, is concerned, former data (reviewed in SOLA *et al.* 2007) regarded only five Mediterranean species, *Liza ramada*, *L. aurata*, *L. saliens*, *Chelon labrosus*, and *Oedalechilus labeo* (Fig. 1). In most of them (four species), the subtelocentric pair is the smallest one of the chromosome complement, chromosome pair number 24. In the fifth species, O. *labeo*, the subtelocentric chromosome pair is larger and classified as chromosome pair number 9. In all species the subtelocentrics have been found to have NORs located on their short arms, by both Ag-staining, CMA_3 and FISH with 18S rDNA.

Considering the chromosome location of 5S rDNA, an interesting picture emerges. In *L. ramada*, *L. aurata*, *C. labrosus*, and *O. labeo* the minor ribosomal genes are located in an interstitial position of a medium-sized chromosome pair which is different from the NOR-bearing chromosome pair. Pursuing a parsimonious criterion, the 5S rDNA-bearing chromosome pair was considered homeologous in all of them and classified as chromosome pair number 8 in all species. In *L. saliens*, in addition to the site on pair number 8, a second site for 5S rDNA was detected, located in a terminal position of chromosome pair number 1. Therefore, comparing the idiogram (Fig. 1) of *L. saliens* to cytotype A shown by *M. cephalus* and *M. liza*, proposed to be the closest to the ancestral one, an alternative and reverse location of major and minor ribosomal genes is observed, so that an event of reciprocal translocation with respect to a common ancestral karyotype might be hypothesized.

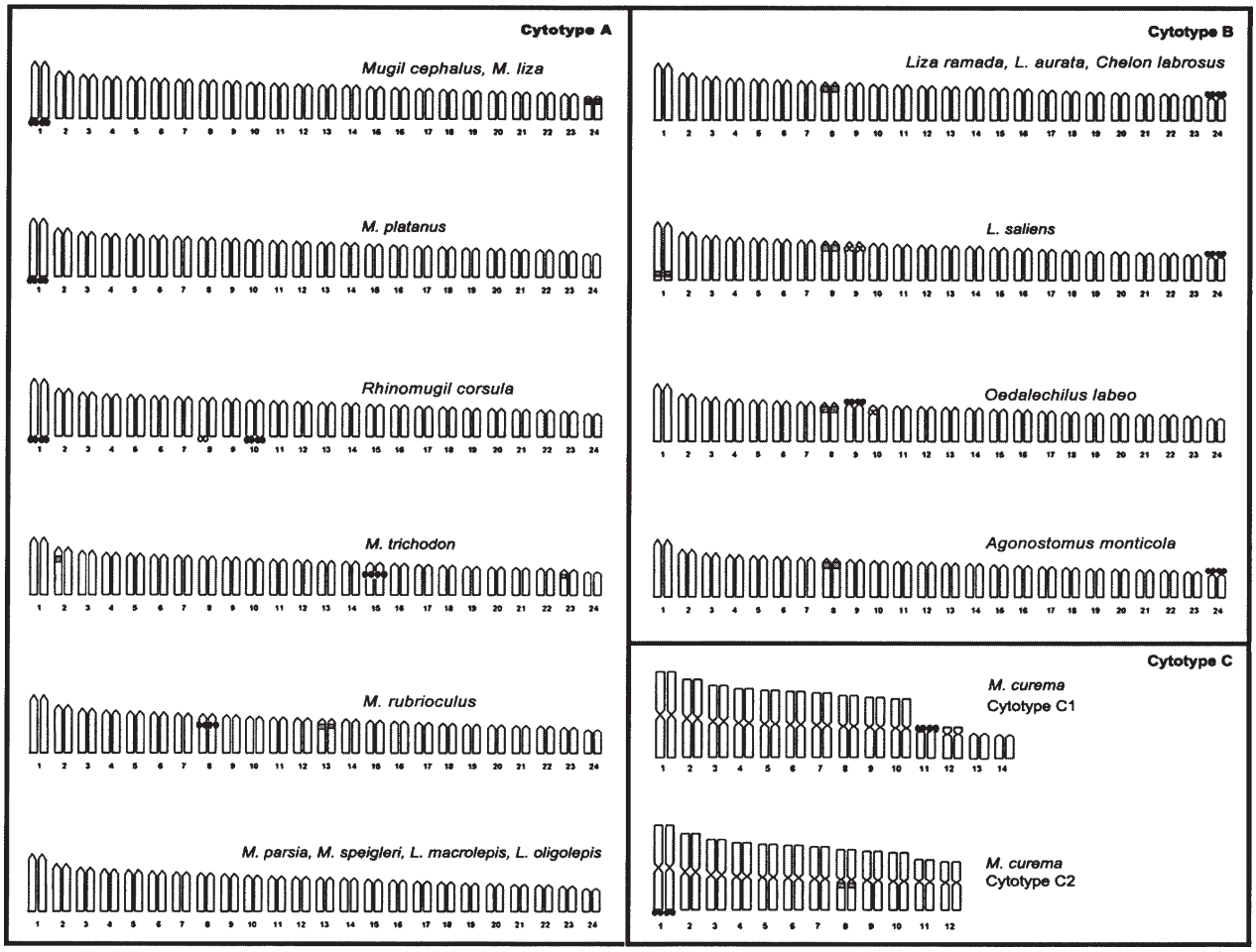


Fig. 1. Idiograms summarizing the karyotypes and the major and minor ribosomal genes locations reported in species of Mugilidae with different cytotypes. For *Liza macrolepis* and *L. oligolepis*, *Mugil parsia*, *M. speigleri* (these two latter later respectively assigned to the genera *Liza* and *Valamugil* - THOMSON, 1997), only the Giemsa stained karyotype is available. For *Mugil platanus*, *Rhinomugil corsula* and *M. curema* cytotype C1, data on NORs are based on Ag-staining only. *M. curema* cytotype C1 is shown by specimens from USA and from Brazil, cytotype C2 by specimens from Venezuela. *Solid circles* represent constant and *open circles* represent additional and variable locations of 18S rDNA. *Grey bars* represent locations of 5S rDNA.

Within this cytotaxonomic picture, the cytogenetic features recently described by NIRCHIO *et al.* (2007) in a species from Venezuela, *Agonostomus monticola*, were found to be different from those which had been foreseen. Indeed, this species belongs to a genus which is considered to be the most primitive among living mugilid (THOMSON 1997), and it was expected to show the chromosome constitution which has, to date, been considered plesiomorphic. On the contrary, though the species shows the 48 all-uniarmed karyotype (Fig. 1), its smallest chromosome pair is subtelocentric, bearing 18S rRNA genes on its short arms. Considering also the 5S rDNA location, interstitially positioned in a medium-sized chromosome pair, *A. monticola* shows an overall apparent similarity in the karyotype constitution, major and minor rDNA loci numbers and locations, to *Chelon labrosus* and three *Liza* species, *L. ramada*, *L. aurata*, and *L. saliens* (see SOLA *et al.* 2007, for references), that is, the karyotype of *A. monticola* can be assigned to cytotype B.

The latter cytotype B is therefore shared by a genus, *Agonostomus*, which is the most basal in the family, and by two other genera which are, on the other hand, considered to be the most advanced in the family (THOMSON

1997). This indicates that cytotype B might be regarded as the plesiomorphic condition for the karyotype in the family. Consequently, cytotype A, shared by most of the species of a genus, *Mugil*, in an intermediate systematic position, and which has been so far considered to be the closest to the ancestor's karyotype, should now to be re-considered as derived. This factor should be taken into consideration in any cytotaxonomic reconstruction of the family.

The analysis of the constitutive heterochromatin location has been so far applied to a limited number of the species with the 48 uniarmed karyotype, four with cytotype A and six with cytotype B (Sola *et al*. 2007; Nirchio *et al.* 2007). Clear chromosome markers, useful for cytotaxonomic considerations, have not been identified, as a generalized pericentromeric location has been observed in all of them. However, preliminary data on the heterochromatin composition in the six Mediterranean species (Sola *et al.* 2007) have suggested the existence of different types of satellite DNA whose analysis might provide a deeper insight into the understanding of the mechanisms of chromosome divergence in Mugilidae.

As far as *M. curema* is concerned, as mentioned before, two cytotypes had been described for specimens from USA (cytotype C1, 2n=28, FN=48; Le Grande & Fitzsimons, 1976) and from Venezuela (cytotype C2, 2n=24, FN=48; Nirchio & Cequea, 1998) (Fig. 1). Recent morphological and cytogenetic data obtained on additional samples and the application of differential staining techniques and FISH revealed additional information on the extent of the chromosome differentiation.

As for the new samples examined, specimens from a farther southern region of the areal of the species, from Paranà, Brazil (Nirchio *et al.* 2005a) have been investigated and found to have the same cytotype C1 shown by specimens from Louisiana (Le Grande & Fitzsimons 1976). Thus, based on geographical considerations and on the coastal habits of the species, it is noteworthy that the farthest away populations (from Louisiana and Brazil) share a similar chromosome complement, which is different from the one found in the population collected at a site (Venezuela) which is geographically intermediate. In addition to this, three specimens from Isla Margarita (Venezuela), collected over a 10 years period, have been found to be characterized by cytotype C1, *i.e*., a cytotype different from the more common cytotype C2 in the area (unpublished data). It is worth to emphasize that individuals with an intermediate karyotype between cytotype C1 and cytotype C2 (i.e., 2n=26) have never been reported from any collecting location.

The same specimens with cytotype C1 from Paraná (Nirchio *et al.* 2005a) have been investigated through Ag-staining, and NORs have been localized on the short arms of the largest subtelocentric chromosome pair (Fig. 1). On the other hand, in specimens with cytotype C2 from Isla de Margarita (Rossi *et al.* 2005), both Ag-staining, CMA_3 and FISH with 18S rDNA show signals, corresponding to NORs, at the terminal region of the largest metacentric chromosome pair (Fig. 1). Thus, NORs do have a different location in the two cytotypes and this identifies a further degree of differentiation between them.

The two cytotypes appear to be further differentiated based on the heterochromatin distribution. Indeed, specimens with cytotype C1 from Brazil display only pericentromeric C-positive regions, whereas specimens with cytotype C2 from Venezuela, in addition to these, show heterochromatic blocks also at the terminal regions of most chromosomes, as well as in an interstitial location in some of them (Nirchio *et al.* 2005a).

In specimens with cytotype C2 (Rossi *et al*. 2005) the 5S rRNA genes have also been localized and found in a subcentromeric position of a medium-sized chromosome pair (Fig. 1). These same specimens have been investigated also for the location of the telomeric sequences, which might have provided insight into Robertsonian rearrangements in the species. However, the telomeric probe hybridized only at the ends of all chromosomes, no pericentromeric or interstitial signals having been obtained. It is worth emphasizing that the absence of additional interstitial telomeric signals is considered to be a stabilizing factor for fusions.

Thus, going back to cytotype A of *M. cephalus* for comparison, the original hypothesis made by Le Grande & Fitzsimons (1976), of a direct derivation of the karyotype of *M. curema* through Robertsonian fusions from an ancestral group with a chromosome complement similar to that of *M. cephalus*, is not really supported. Indeed, neither cytotype C, compared to cytotype A, has cytogenetic features compatible with the original hypothesis: cytotype C1 because of its different location of NORs; cytotype C2 because of its different location of 5S rRNA genes, clearly not located on the smallest

chromosome pair of the chromosome complement. Nor a direct cytotaxonomic relationship between the two cytotypes C can be inferred.

FROM NOW ON

Obviously, the question arises as to whether data are disclosing an intraspecific polymorphism or the existence of two - or three - different species. All these cytogenetic features prompted the morphological reexamination of Venezuelan and Brazilian samples with the two different cytotypes, and preliminary data suggest that, indeed, we are dealing with two different species (NIRCHIO *et al.* 2005a). Similarly, the three specimens with cytotype C1 from Isla de Margarita were found to be morphologically different from both the sympatric specimens with cytotype C2 and specimens from Brazil with the same cytotype C1 (unpublished data). Thus, the whole cytogenetic and morphological data strongly support the existence of a species complex in *M. curema*. Cytogenetic analyses of additional samples, as well as additional analyses with other molecular markers, *i.e.*, nuclear or mitochondrial sequences, are needed to clarify the magnitude of the genetic divergence and, thus, the systematic position of populations with different cytotypes. This will provide the basis for the formal description of possible cryptic species.

In conclusion, the available data, on the one hand, suggest that karyological studies on the remaining undescribed species of Mugilidae be carried out in order to provide a more general picture of karyoevolutive trends in the family. On the other, the current picture stimulates researchers to go beyond the current available cytogenetic markers, and this will bring the study of chromosomal evolution in Mugilidae into the future. Indeed, the cytogenetic features of the family so far available appear to offer a great opportunity both for cytotaxonomic and phylogenetic studies, as well as for structural, evolutionary and functional analyses of the genome, *i.e.* for a cytogenomic approach.

In this context, on the one hand, the isolation and cloning of additional satellite DNA families are being carried out to study their chromosomal location of the Mediterranean and Caribbean species. On the other, the production of chromosome-specific painting probe is being pursued. This implies the isolation, by laser micro-dissection, followed by DOP-PCR amplification, of an entire marker chromosome to be used as a probe in cross-hybridization FISH experiments between different species, belonging or not to the same genus and/or to the same or a different geographic area. This will allow the investigation on inter-specific homologies, on the degree of synteny conservation, and on the structural changes that led to the divergence of mullets chromosome complements.

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