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Genetic evolution and diversity of common carp *Cyprinus carpio L.*

Review Article

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Abstract: Knowledge of genetic variation and population structure of existing strains of both farmed and wild common carp *Cyprinus carpio* L. is absolutely necessary for any efficient fish management and/or conservation program. To assess genetic diversity in common carp populations, a variety of molecular markers were analyzed. Of those, microsatellites and mitochondrial DNA were most frequently used in the analysis of genetic diversity and genome evolution of common carp. Using microsatellites showed that the genome evolution in common carp exhibited two waves of rearrangements: one whole-genome duplication (12-16 million years ago) and a more recent wave of segmental duplications occurring between 2.3 and 6.8 million years ago. The genome duplication event has resulted in tetraploidy since the common carp currently harbors a substantial portion of duplicated loci in its genome and twice the number of chromosomes (n =100-104) of most other cyprinid fishes. The variation in domesticated carp populations is significantly less than that in wild populations, which probably arises from the loss of variation due to founder effects and genetic drift. Genetic differentiation between the European carp *C.c. carpio* and Asian carp *C.c. haematopterus* is clearly evident. In Asia, two carp subspecies, *C.c. haematopterus* and *C. c. varidivlaceus*, seem to be also genetically distinct.

Keywords: *Common carp • Microsatellites • Mitochondrial DNA markers • Genome evolution • Genetic diversity • Population*

Abbreviations

AFLP - amplified fragment length polymorphism;
EST - expressed sequence tag;
mtDNA - mitochondrial DNA;
PIC - polymorphism information content;
PCR - polymerase chain reaction;
RAPD - random amplification of polymorphic DNA;
RFLP - restriction fragment length polymorphism;
SNP - single nucleotide polymorphism.

1. Introduction

Common carp (*Cyprinus carpio* Linnaeus 1758) belongs to the family Cyprinidae (minnows) which is considered the largest freshwater fish family [1]. The carp is established as one of the oldest domesticated fish species. In China, carp farming began in the 5th century B.C., whereas the culture of carp in Europe dates back to the Roman Empire [2]. The wild ancestor of domesticated carp probably lived in the Caspian and Aral Sea basins, from where it was dispersed both to Western Europe and to East Asia [3]. The current natural distribution of common carp ranges from Europe throughout the continent of Eurasia to China, Japan and South East Asia (Figure 1).

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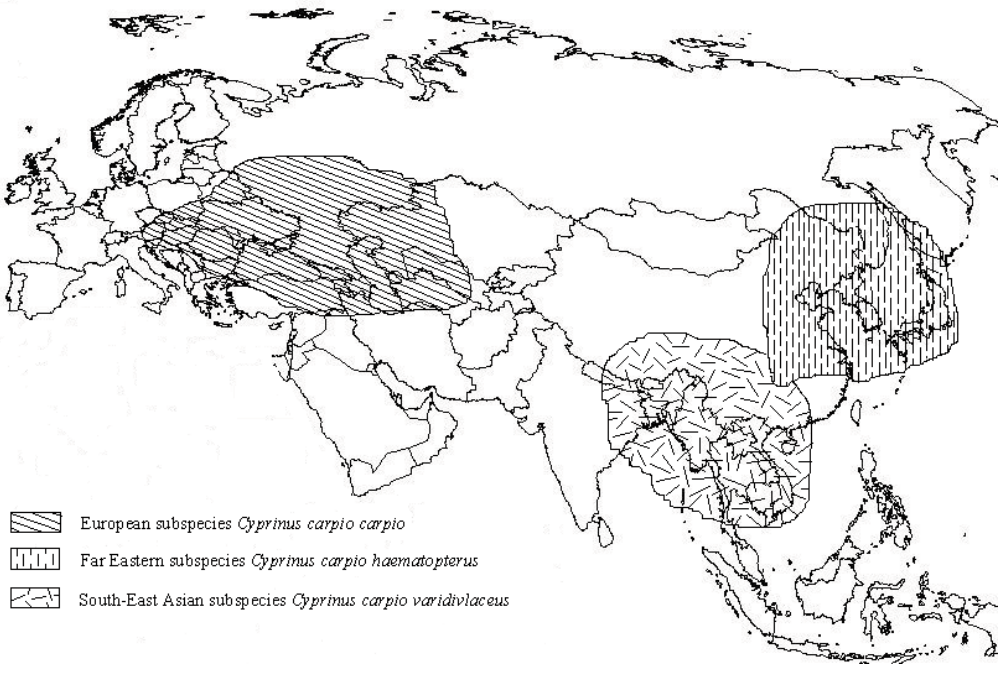

Figure 1. Ranges of wild common carp populations in Eurasia.

There is a long history of changes in common carp taxonomy. According to the relatively recent taxonomic reports, Kirpitchnikov [4] recognized four subspecies of carp: *C. carpio carpio* (Europe), *C. c. aralensis* (Central Asia), *C. c. haematopterus* (East Asia) and *C. c. viridiviolaceus* (South East Asia). In contrast, Balon [3] suggested that only two subspecies could be clearly recognized: *C. c. carpio* (Europe) and *C. c. haematopterus* (East Asia). Kirpitchnikov [5] then questioned the validity of *C. c. viridiviolaceus.* Most recently, Kottelat [6] considered the common cultured carp in South East Asia to be a distinct species, *C. rubrofuscus*.

Relatively recent advances in molecular biology, principally in the development of the polymerase chain reaction (PCR) for amplifying DNA, automated DNA sequencing and data analysis, have resulted in robust techniques that have been subsequently applied for screening, characterization, and evaluation of genetic diversity of a variety of species including common carp. Using genetic markers allows the precise dissection of a population structure, which is often unachievable with the use of morphologic markers alone. Knowledge of genetic variation and population structure is absolutely necessary for any efficient fish management and/or conservation program. In this review, we consider current knowledge about genetic diversity and evolution of common carp genome revealed by the analysis of various molecular markers.

2. Molecular markers

To study the genetic diversity of common carp, several types of polymorphic markers have been analyzed. These include both protein (*i.e.* allozymes) [7,8] and DNA-based markers such as microsatellites [9-11], amplified fragment length polymorphisms (AFLPs) [10,12], restriction fragment length polymorphisms (RFLPs) [13,14], random amplification of polymorphic DNA (RAPD) [15], and mitochondrial DNA (mtDNA) variability [16,17]. Advantages and disadvantages of using each marker type in the aquaculture research have been thoroughly reviewed by Liu and Cordes [18] and hence are beyond the scope of this review.

Microsatellites and mtDNA markers have been most frequently exploited in the analysis of the common carp genetic diversity. By the end of 2008, of nearly 1700 annotated nucleotide sequences of the common carp deposited to GenBank, 290 sequences could be attributed to microsatellites [12,19-22]. Almost all of them (95%) have been recently developed in the Heilongjiang Fisheries Research Institute (Harbin, China) [23]. The extreme popularity of microsatellites in the population analysis arises from the selective neutrality of these markers and easy replication and comparability of microsatellite-based data in various populations. Microsatellites are particularly helpful for the assessment of biodiversity of domesticated strains

and lineages at regional level while using mtDNA markers may take advantage while applying in broad-scale population analyses.

Because mtDNA has a high substitution rate and effective population size of approximately one-quarter of that of nuclear markers [24], it allows a chance of recovering the pattern and tempo of recent historical events without an extensive sequencing effort. Highly variable sections of mtDNA evolve much faster compared with nuclear DNA and are consequently a powerful tool for establishing the levels of genetic diversity and phylogenetic structure within a species [25]. The mitochondrial genome of carp has been completely sequenced [26]. The carp mtDNA comprises 16,575 bp and contains the same set of genes (13 proteins, 2 rRNAs, and 22 tRNAs) as do other vertebrate mitochondrial DNAs [26]. Certain highly variable regions of mtDNA such as D-loop, 16S rRNA, cytochrome *b*, ND3/4, ND5/6, and MTATPase6/MTATPase8 were used for study of the biodiversity of common carp by direct sequencing or PCR-RFLP analysis [16,17,27-29].

3. Evolution of common carp genome

Common carp has a very high number of chromosomes (n =100-104), approximately twice the number of most other cyprinid fishes [30]. As the carp also has a high DNA content, it was proposed to be tetraploid [31]. About 52% of common carp enzymes showed a pattern consistent with duplication thereby supporting a tetraploidization hypothesis [32]. The finding of duplicated genes also supports this hypothesis [33-35]. Based on the evidence that tetraploid catostomids (suckers) diverged from cyprinids around 50 million years ago [36], the carp tetraploidy was assumed to be of similar age [37]. However, more recent sequence analyses of duplicate loci in common carp revealed that the tetraploidization occurred much later, *i.e.* around 16-19 million years ago [38] (Figure 2). Using analysis of microsatellites, David *et al*. [39] estimated the time of tetraploidization to be about 12 million years ago, close to the estimations of Larhammar and Risinger [38]. David *et al.* [39] also showed that the genome evolution in common carp exhibited two waves of rearrangements: one whole-genome duplication (12 million years ago) and a more recent wave of segmental duplications occurring between 2.3 and 6.8 million years ago. Assuming the age of 12 million years ago, this would be one of the most recent genome duplications among vertebrates.

The common goldfish *Carassius auratus* is closely related to the common carp as it has the same number of chromosomes [40] and can form naturally occurring hybrids [41]. This strongly suggests that goldfish and common carp diverged from each other after the tetraploidization event (Figure 2). The absence of pseudogenes among common carp genes cloned to date agree with the previous suggestions that after tetraploidization the duplicate genes may continue to be expressed for millions of years [42]. Thereby, they can evolve as a pool of expressed genes towards acquiring modified or new functions. For example, common carp

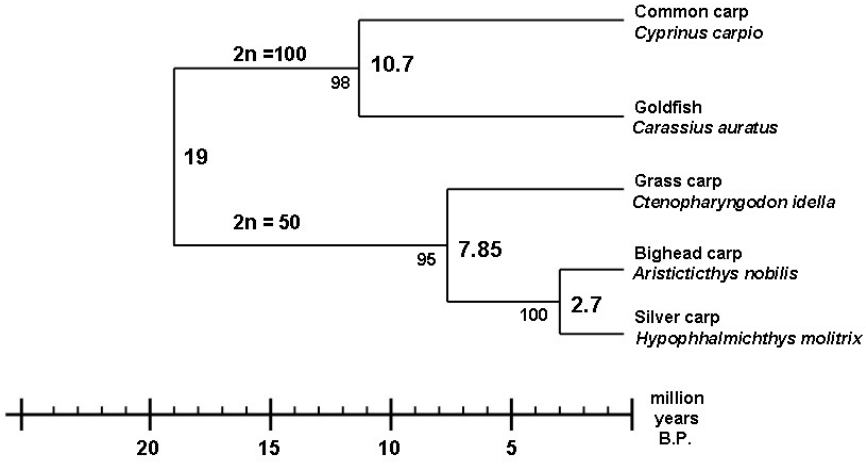

Figure 2. Evolutionary tree for tetraploid common carp and four other cyprinids. Divergence times were calculated from the divergence at silent sites and are based on the DNA sequence of the somatotropin gene. Tetraploidy arose 19 million years ago and resulted in the divergence of tetraploid cyprinids such as common carp and goldfish from diploid cyrpinids (grass carp, bighead carp, silver carp, and others). Numbers outside the nodes are bootstrap values (%), and those inside nodes are estimates for divergence time. Adapted from Larhammar and Risinger [38].

expresses two hepatic stearoyl-CoA desaturase genes, which share 89% and 65% identity at the amino acid and nucleotide levels, respectively [43]. Both genes are functional 9-desaturases, but one is regulated by dietary fatty acid composition [43] whereas the other is regulated by temperature [44], consistent with divergence of the promoter regions controlling expression [45].

The molecular mechanism of tetraploidization (through allotetraploidization, *i.e*. species hybridization, or through genome doubling) in common carp is still speculative. A supportive evidence in favor of allotetraploidization comes from cytogenetic experiments showing lack of quadrivalents in meiotic nuclei and no losses of chromosomes in the duplication event [31]. The ability of closely related goldfish and common carp (or crucian carp and common carp) to form fertile allotetraploid interspecies hybrid progeny [46] suggests allotetraploidization as a possible mechanism of species formation. The carp has a doubled number of chromosomes in two distinct, although similar, sets as suggested by the identification of paralogs using the PCR method. Evolution of polyploid genomes makes the distinction between allotetraploidy and autotetraploidy based on disomic inheritance, more difficult as time elapses [47]. In light of the relatively short time since tetraploidization of the carp, the disomic inheritance is suggested in carp to result from allotetraploidization rather than by diploidization of an autotetraploid genome [38,39]. This evidence is supported by recent data of Zhang *et al.* [48] who studied the segregation pattern of microsatellites in a gynogenetic family of common carp.

4. Genetic diversity of common carp

Common carp has a long history of domestication and numerous strains and breeds have been developed from its ancestor, the wild common carp, *Cyprinus carpio*, both in Europe and Asia. The natural distribution range of wild carp in Eurasia is nowadays divided into distinct western (Caspian, Aral and Black Sea basins) and eastern (East and South-East Asia) areas, which were supposedly isolated during multiple Pleistocene glaciations [5]. The use of molecular markers showed a clear genetic divergence between the European and East Asian carp [27,28,49] therefore suggesting the existence of at least two subspecies, *C. c. carpio* and *C. c. haematopterus*, formerly distinguished on the basis of morphological differences [3-5].

In all European carp populations studied, no difference between their mtDNA markers was found therefore suggesting for a relatively recent bottleneck in the history of the European carp [50,51]. A single origin of the European carp from a common ancestor with the Central Asian carp was finally proved by Memis and Kohlmann [52] who closed a geographic gap in sampling locations between European and Central carp subspecies. The habitat place of the ancestral European carp was not well defined in any single study. However, several reports referred to the Danube drainage as the region invaded by European carp ancestors came from the Caspian basin refugia in the postglacial period [50,51]. Assuming the mutation calibration rate of 0.76% divergence per million years for cyprinid mtDNA [53], splitting between the European and Asian carp subspecies from the common ancestor is estimated to take place around 500,000 years B.P., *i.e.* already before the Weichselian glaciation period [13].

Although common carp has been cultivated in ponds of Europe for several hundred years [54], the origin of the European domestic common carp was debated. Assuming the long cultivation history of common carp in Asia, some scientists postulated that the ancestor of the European domestic carp was the Asian common carp transferred from Asia to Europe during ancient Greek and Roman periods [55]. However, others considered a German domestic strain of common carp as the first improved carp that appeared after the domestication of a wild common carp in the Danube River in the 17th and 18th centuries [37]. Using allozymes and mtDNA markers revealed different ancestors for domestic carp in Europe: the German mirror carp was domesticated from European subspecies *C. carpio carpio*, while the Russian scattered scaled mirror carp originated from Asian subspecies *C. carpio haematopterus* [27,28,49]. Similarly, Desvignes *et al.* [56] observed a clear difference between western strains cultivated in France and the Czech Republic and the Ropsha carp originated from the Asian Amur wild carp.

In Russia, significant difference was observed between strains of common carp cultivated in Eastern Europe (Hungarian, Angelinskii, Cherepetskii, Stavropol, Ropsha) and the Amur wild common carp as revealed by RAPD markers [15]. Interestingly, the analysis with mtDNA showed that the Amur carp holds mtDNA haplotypes, one of those is very close to that of the European carp while another one is almost identical with that of the East Asian carp [16,50].

Based on these data, Froufe *et al.* [50] speculated on an Asian origin of the European carp. However, the converse possibility that the European carp has been introduced to China [3] is also consistent with the data. Findings of Froufe *et al.* [50] are likely to be biased by a small sampling size of the Amur carp (n = 5) and rather reflect the current admixture in populations of the Amur wild carp affected by modern transplantations.

Among morphologically distinctive red carp strains cultivated in China, *C. c*. var *singuonensis* and *C. c.* var. color might have originated from one monophyletic group, while *C. c.* var. *wananensis and C. c.* var. *wuyuanenesis* might have originated from an independent evolutionary branch as revealed with the help of mitochondrial markers [57]. The Xingguo domestic red carp (*C.c.* var. *xingguonensis*) showed the highest variability (as shown by microsatellites) compared to other carp strains farmed in China [9].

In South East Asia, the validity of a common carp subspecies *C. c. viridiviolaceus* initially recognized by Kirpitchnikov [4] was later questioned [3,5]. Kottelat [6] distinguished the common cultured carp in South East Asia as a separate species, *C. rubrofuscus*, although this is disputed by Nguyen and Ngo [58] who considered this species to be quite rare. Using mtDNA analysis, Thai *et al.* [16] found that Vietnamese and Indonesian carp strains are genetically distinct from European, Chinese and Japanese strains thereby supporting the Kottelat's taxonomy [6].

As documented by breeders in the Niigata Prefecture, the Japanese ornamental carp (koi), a colored variant of the common carp, was developed in the early 19th century [3]. Genetic studies involving mtDNA showed that Koi carp has similar lineage with the Chinese color carp [16,59]. This finding supports the origin of the Japanese carp from the Chinese color carp, which has a long history of domestication that can be traced back over 1200 years [59]. Within the Koi carp, a lowest genetic variability was found in monochromatic strains (black koi and white koi). These breeds have been bred within strains to produce similar progeny, from which the most desirable individuals were then selected for future broodstock [10]. The broodstock is maintained by breeders as small populations that explains its low variability. In contrast, colored strains of koi such as Kohaku, Sanke, and Showa are usually crossed within and among variants, and larger populations are maintained as broodstocks. This explains the higher levels of polymorphism and genetic similarity among these three breeds observed by David *et al*. [10]. In their study of wild carp captured from 11 different Japanese localities, Mabuchi *et al*. [17] revealed a high percentage of non-native mtDNA haplotypes. The mtDNA haplotypes are originated from domesticated strains introduced from continental Eurasia, except for a distinct cluster of haplotypes related to the Lake Biwa wild strain, an ancient natively conserved Japanese carp [60,61].

For both European and Asian carp, genetic diversity in domesticated populations was shown to be significantly lower than that in wild populations [29,51,62]. For European carp, Kohlman *et al.* [51] found an average number of alleles per microsatellite locus of 4.4 in populations of farmed carp *vs*. 8.2 in wild caught populations. Similarly, Thai *et al*. [29] analyzing Vietnamese strains of common carp observed 5.8 alleles/locus in experimental carp lines compared to 9.3 alleles/locus in wild populations. Interestingly, loss of genetic diversity in hatchery populations was also found in other aquaculture species such as channel catfish [63], Atlantic salmon [64], brown trout [65], and Japanese flounder [66]. Loss of variation in closed hatchery populations can occur during establishment (founder effects) and over subsequent generations through genetic drift arising from the low effective broodstock number [67]. The large reduction in genetic variability in farmed carp indicates the potential negative impact of captive breeding on domesticated common carp stocks. Thus, the low levels of genetic variation most likely reflect difficulties in the genetic management of broodstock leading to the low effective size in populations of farmed carp.

5. Concluding remarks

The use of multiple data sets and information from different molecular markers is becoming more common in aquaculture research. An example for common carp is the study of Kohlman *et al*. [13] who used allozymes, microsatellites, and mtDNA to analyze variation and taxonomic issues. Among molecular markers, microsatellites and mtDNA are most frequently used. Wide popularity and high utility of these markers results from the fact that both are based on known nucleotide sequence information. This facilitates the reproduction and subsequent comparison of molecular data sets generated with mtDNA markers and microsatellites in different populations and studies. For example, high efficiency of microsatelltes could be supported by results of Thai *et al*. [29] who used only four microsatellites for analysis of the diversity in 20 population samples of common carp from different regions of Vietnam. Using the microsatellites, Thai *et al*. [29] successfully distinguished between the Vietnamese experimental line and wild populations from the introduced Hungarian and Indonesian carp lines thereby showing possibility to determine the affinities of the hatchery stocks and the extent to which they represent mixed stocks.

The population data obtained with help of microsatellites and mtDNA are highly concordant as supported by results of Thai *et al*. [29,68] obtained in analysis of the population structure and diversity of different Vietnamese strains of common carp. However, the extent of differentiation was much greater for the mtDNA (Fst=86.30%) compared with that of

the microsatellite data (Fst=23.80%) [29], thereby suggesting that mtDNA is more suitable (compared to microsatellites) for the detection of population mixing and for elucidating the origin of the stocks contributing to the mixing. However, the power of microsatellite analysis in assignment tests may be increased by recruiting additional loci, which is not the case for mtDNA since all the mtDNA markers are linked.

In the duration of a long history of domestication, common carp has been subjected to all kinds of genetic interventions including selective breeding, chromosome manipulations, sex reversal, and transgenesis [69-72], which resulted in producing a variety of breeds, strains and hybrid fish. Although the number of studies assessing the genetic variability and phenotype performance with help of molecular markers continually grows, a vast majority of domesticated carp strains remain to be genetically characterized. Local wild common carp stocks, like those of many fish species, are under threat from a number of processes including environmental degradation that occurs in Uzbekistan [73], or the invasion of "exotic" genotypes into natural populations of Japanese carp as a result of domestication and translocation [17]. As assessed with molecular markers [68], Vietnamese common carp is relatively genetically homogeneous, and indeed could potentially represent a unique genetic resource for common carp that needs to be conserved. Exploiting molecular markers should provide comprehensive DNA-based data sets to be collected at a regional level for common carp and then be essential for the effective management of domesticated and wild carp stocks in every carp-producing country.

In microsatellite-based population analyses, researchers typically used markers developed by Crooijmans *et al.* [19], although it was common to use sets of markers that differed from study to study. For example, Memis and Kohlman [52] used a set of four microsatellites (MFW1, MFW6, MFW7, and MFW28), which was similar with that used by Lehoczky *et al.* [74] for assessment of the diversity of Hungarian farmed carp strains cultivated in Szarvac, but was different from the marker sets exploited by Desvignes *et al.* [56] (MFW7, MFW13, MFW16, MFW29), Thai *et al.* [29] (MDW1, MFW6, MFW7, MFW28), and Jewell *et al.* [62] (MFW13, MFW17, and MFW28). Microsatellites MFW1, MFW9, and MFW13 have been mapped to the same linkage group LG49 [75] and hence their simultaneous application in a single set could bias the parentage analysis of a farmed broadstock due to a likely cosegregation between the markers. Thus, implementation and comparison of standardized sets of markers (nuclear DNA markers should be unlinked) among aquaculture geneticists across the range of common carp is highly recommended.

Application of new types of molecular markers such as type I (coding) markers, including single nucleotide polymorphisms (SNPs) and polymorphic expressed sequence tags (ESTs), is highly recommended. This will strengthen the performance of molecular analysis of population dynamics of wild and farmed carp, detection of footprints of divergent selection, and searching adaptive and fitness-related traits [76]. Unfortunately, there are no publicly available reports on using type I (coding) markers in studies of the population genetics of common carp. Until recently, the value of EST resources was perhaps underestimated in the aquaculture genetics community, primarily because of the lack of bioinformatics capabilities. However, by the end of 2008, more than 32,000 common carp EST sequences have been deposited to the GenBank nucleotide database [77]. These sequences represent a substantial source for *in silico* extraction and further validation of SNPs using an appropriate technique [22,78]. Also, as with any cyprinid fish, there is great potential in applying information from the zebrafish genome [79] to the carp, as this provides a putative sequence source for the majority of coding genes in common carp.

Recent advances in bioinformatics tools, such as the HaploSNPer web-based program for SNP mining [80], are expected to greatly facilitate progress in SNP discovery for common carp.

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