

Review Article

A Review of Pangasiid Catfish Genomics for Conservation and Aquaculture: Current Status and Way Forward

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ABSTRACT

Due to its ecological and economic importance, the family Pangasiidae has been the focus of considerable biological and genetic research. This family includes thirty species of catfish distributed among four genera: *Helicophagus*, *Pangasianodon*, *Pangasius*, and *Pseudolaia* within the order Siluriformes. In recent years, genomic-scale data for a wide range of aquatic species have been more easily available and accessible through next-generation sequencing. Draft genome sequences of numerous fishes have been the basis for many downstream investigations. However, although genomic-based technologies allow for the collection of robust data, there is a dearth of research on pangasiid catfishes, which could

potentially enhance fisheries' management and aquaculture. To realise its aquaculture potential and strategise the conservation of this family, fundamental knowledge of its biology, genetics, and genomics, among others, is critical. This review focuses on the current molecular knowledge of the family Pangasiidae, the remaining gaps, and the challenges faced in closing these gaps.

Keywords: Aquaculture, conservation, genomics, mitogenome, Pangasiidae

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AN OVERVIEW OF FAMILY PANGASIIDAE

The family Pangasiidae has been the subject of considerable biological and genetic research due to its ecological and economic significance in aquaculture. A tremendous diversity of this family is found in Southeast Asia (Vietnam, Thailand, Laos, Cambodia, Myanmar, Peninsula Malaysia, Borneo, Java, and Sumatra), with additional species in India and China (Fricke et al., 2023; Froese & Pauly, 2024; Kottelat, 2013; Parenti & Lim, 2005; Roberts & Vidthayanon, 1991). Members of this family are usually found in freshwater, but several species inhabit brackish and marine environments as part of their life cycles (Gustiano, 2009; Roberts & Vidthayanon, 1991; Vu et al., 2020). In Malaysia, species of this family are collectively known as ‘Patin’.

The pangasiids represent a diverse species composition of 30 valid species within four genera (Figure 1): *Helicophagus* (3 species), *Pangasianodon* (2 species), *Pangasius* (23 species), and *Pseudolais* (2 species) (Fricke et al., 2023; Froese & Pauly, 2024; Gustiano, 2009; Kottelat, 2013). Adult pangasiid catfishes can be identified by their laterally compressed bodies, two sets of barbels (maxillary and mandibular), a long anal fin, a short dorsal fin with strong spines, a small adipose fin that is never confluent with the caudal fin, and smooth skin (Froese & Pauly, 2024; Gustiano, 2009; Roberts & Vidthayanon, 1991). The dominant genus, *Pangasius* (76%), occurs in the Indo-Malay Archipelago (IMA) and Indo-China

hotspot regions of Peninsula Malaysia, Borneo, Indonesia, Thailand, Cambodia, and Vietnam. These distribution ranges had been mapped based on combined pieces of literature (Froese & Pauly, 2024; Gustiano, 2009; Inger & Chin, 1962; Kottelat, 2013; Roberts & Vidthayanon, 1991). This genus is characterised by the presence of long maxillary barbels, six-branched pelvic-fin rays, and pectoral and adipose fins that are relatively robust (Froese & Pauly, 2024; Gustiano, 2009; Roberts & Vidthayanon, 1991).

Members of the pangasiid family are mainly distributed in lakes and river basins (Figure 1). Peninsular Malaysia (Perak and Pahang Rivers), Borneo (Batang Rajang, Kinabatangan, Kayan, Berau, Mahakam, Barito, Kahayan and Kapuas Rivers) and Sumatra (Indragiri, Musi, Batang Hari and Way Rarem Rivers) harbour three genera including *Helicophagus*, *Pangasius*, and *Pseudolais*. The Indochina regions (Chao Phraya, Mae Klong, Hue, and Mekong Rivers) have all four genera, while Java (Ciliwung, Solo, and Brantas Rivers) has only two genera (Figure 1). Their conservation status is considerable. Several are commonly found throughout the pangasiid home range, while others are globally or locally threatened.

Species distributions of pangasiids have been extensively studied since the 1990s, thanks to a multitude of sampling initiatives across Southeast Asia. In Indo-China, 13 species were inhabit the Mekong River, Chao Phraya River, and Mae Klong River (*Helicophagus leptorhynchus*,

Pangasianodon gigas, *Pangasianodon hypophthalmus*, *Pangasius bocourti*, *Pangasius conchophilus*, *Pangasius elongates*, *Pangasius krempfi*, *Pangasius larnaudii*, *Pangasius macronema*, *Pangasius mekongensis*, *Pangasius sanitwongsei*, *Pseudolais micronemus*, and *Pseudolais pleurotaenia*) (Figure 1) (Fricke et al., 2023; Froese & Pauly, 2024; Roberts & Baird, 1995; Roberts & Vidthayanon, 1991). The Malaysian waters are home to several catfish species. Eight species are native to Malaysian rivers. Three of these native species (*Helicophagus waandersii*, *P. micronemus*, and *Pangasius nasutus*) inhabit the major rivers of Peninsula Malaysia, the Pahang River, while *P. micronemus* can also be found in Perak and the major Borneo rivers of Batang Rajang, and Kinabatangan (Baharuddin, 2016; Gustiano, 2009; Roberts & Vidthayanon, 1991). Moreover, *P. nasutus* was also reported in Batang Rajang (Parenti & Lim, 2005). In addition, five more species occur in the Batang Rajang and Kinabatangan rivers (*Pangasius polyuranodon*, *Pangasius humeralis*, *Pangasius lithostoma*, *Pangasius kinabatanganensis*, and *Pangasius sabahensis*). The latter four are believed to be endemic to Borneo (Gustiano & Pouyaud, 2005; Kottelat, 2013; Parenti & Lim, 2005). It is not unexpected as the freshwater fish fauna of northwestern Borneo, which includes Sarawak, Sabah, and Brunei, is known for its high degree of endemism (Parenti, 1996; Parenti & Lim, 2005).

Inland fisheries in Borneo are important, mostly along rivers, with the rest from lakes, reservoirs, and flood plains (Inger & Chin, 1962; Parenti & Lim, 2005). They have a significant impact on the rural community's economic well-being by creating jobs and investment opportunities, apart from providing abundant sources of protein. However, although these inland fish resources offer low-cost sources of food and nutrition for the people, they make very little contribution to total fishery production and export values due to their low production (Chong et al., 2010; Inger & Chin, 1962).

Despite its importance, this family has relatively limited genomic information, acknowledged as one of the important current perspectives for accelerating the aquaculture industry. A few reviews have been documented, mainly focused on biological diversity, taxonomy and systematics, aquaculture and phylogeographic relationships (Legendre, 1998; Pouyaud et al., 1998; Roberts & Vidthayanon, 1991). Given the present scenario of rapid population declines, coupled with the higher demand for affordable fish protein worldwide, a holistic understanding of the pangasiid family is necessary. While previous studies have provided important knowledge for the first step towards addressing this problem, more work needs to be done, particularly in genomics. This review could serve as a reference for future research efforts in conserving the pangasiid family in the biodiversity hotspots of Southeast Asia based on molecular approaches.

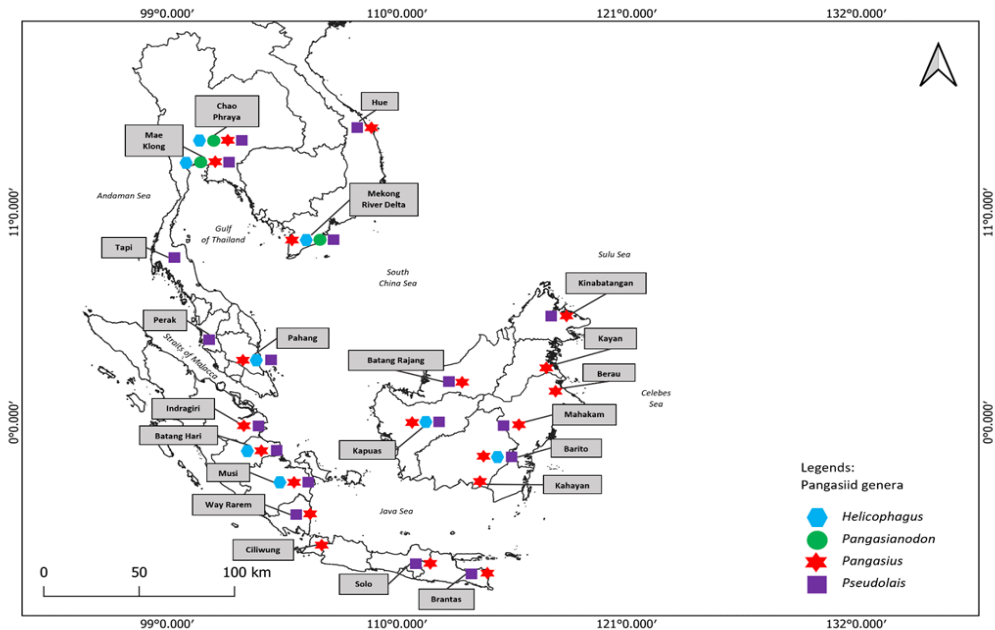


Figure 1. Range distribution of catfish family of Pangasiidae based on genera throughout the Southeast Asia river basins regions

Note. The box shape indicates river location; The shapes colour indicates genera of family Pangasiidae

THE INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN) RED LIST STATUS OF PANGASIID SPECIES

Several pangasiids are common throughout their home range, while others are globally or locally threatened. Based on the IUCN Red List (IUCN, 2023), two species, *P. gigas* and *P. sanitwongsei*, are classified as Critically Endangered (CR) in the Mekong and Chao Phraya Rivers (Jondeung et al., 2007; Sriphairoj et al., 2007, 2018). *Pangasianodon hypophthalmus* is categorised as Endangered (EN), while *P. krempfi* is Vulnerable (VU) (Duong, Nguyen, et al., 2023; IUCN, 2023). In addition, *Pangasius rheophilus*, a native species from Kalimantan, Indonesia,

has also been recently classified as Near Threatened (NT) (Gustiano & Pouyaud, 2005; IUCN, 2023). The common factors that explain the species declination in all these regions include over-harvesting/over-fishing, by-catch, habitat loss/degradation, habitat fragmentation, pollution, human disturbance, and endemism (Chong et al., 2010; Gustiano & Pouyaud, 2005; Inger & Chin, 1962; Parenti & Lim, 2005).

In the Malaysian scenario, *H. waandersii* (Patin Muncung), *P. nasutus* (Patin Buah), *P. kinabatanganensis*, and *P. polyuranodon* are classified as Moderately Threatened (MT), which is equivalent to Endangered (EN) in IUCN 2023 (Chong et al., 2010). The leading causes have been attributed to overharvesting and habitat degradation;

however, in the case of *P. kinabatanganensis*, it is believed to be due to overharvesting on this endemic species. According to Moyle and Leidy (1992), freshwater species that have adapted for life in large rivers or are endemic are in high danger of extinction. On the other hand, estuarine fishes are more likely to be threatened due to their reliance on freshwater inflows (Vu et al., 2020). Considering the threatened status of several species, a comprehensive understanding of several pertinent aspects of the pangasiids is critical. Given the broader implications of continuous habitat degradation to fish productivity, habitat conservation is tightly linked to fish conservation and should be considered an essential fishery management objective. However, it must go in parallel with an updated assessment of the species' conservation status.

ADVANCES IN GENOMIC RESEARCH ON CATFISH SPECIES

The primary goal of genomics research is discovering how the genome functions. Fundamental genome information permits the identification of potential species for aquaculture (Liu, 2007) with desirable traits for production, strengthening resistance to diseases and improving growth rates, thus ensuring the long-term sustainability of aquaculture practices. Therefore, it is essential to understand and interrogate the genetic structure and organisation of a potential aquaculture species and its genomic variants to understand its functional properties (Lu & Luo, 2020; The Aquaculture Genomics, Genetics and

Breeding Workshop et al., 2017; Yue & Wang, 2017). The freshwater aquaculture sector relies heavily on catfish for its numerous advantageous traits, making the study of their genome a priority (Jin et al., 2016; Kim et al., 2018; Wang, Su, et al., 2022). Several species have been farmed, and there are many candidate species for farming and breeding. Ongoing research endeavours have been initiated in the domain of genomic studies in catfish species, yielding noteworthy progress in this study area.

Whole Genome Sequencing (WGS)

Knowledge of the whole genome of an organism, which covers all of its genetic material, including both the coding and non-coding regions, is the ultimate data to explore the full potential of a species for an aquaculture programme (Goodwin et al., 2016; Liu, 2007). By sequencing the complete catfish genome, researchers will have a holistic and deeper grasp of the genetic variation present in each fish. Whole genome sequencing of several catfish species has furnished some breakthroughs. The channel catfish (*Ictalurus punctatus*) (Jin et al., 2016; Liu et al., 2016) and the striped catfish (*P. hypophthalmus*) (Gao et al., 2021; Hai et al., 2022; Kim et al., 2018) genomes were among the first catfish genomes to be sequenced. These genome sequences have provided valuable information for researchers in various fields, including aquaculture and conservation (Jin et al., 2016; Liu, 2007; Lu & Luo, 2020; The Aquaculture Genomics, Genetics and

Breeding Workshop et al., 2017). WGS is increasingly becoming one of the most utilised applications in the next-generation sequencing (NGS) approach. Through this technology, researchers can acquire the most extensive understanding of genomic data and its related biological impacts (Goodwin et al., 2016; Liu, 2007).

These draft genome sequences have served as the basis for a plethora of investigations, such as resource assessment, resistance to disease, growth performances, sex determination, fisheries management, and environmental adaptation (Hai et al., 2022; Jin et al., 2016; Lu & Luo, 2020; The Aquaculture Genomics, Genetics and Breeding Workshop et al., 2017) in key aquatic species. For instance, the genome of Channel catfish (*I. punctatus*), the most cultured species in the U.S., has been widely investigated to understand evolution and important biological characteristics (Jin et al., 2016). Another species of catfish that has been widely explored for its whole genome sequence is *Ictalurus furcatus* (blue catfish) (Wang, Su, et al., 2022), which currently serves as a reference sequence for the study of other blue catfish for various purposes, i.e., gene expression, chromosome inversion, and single nucleotide polymorphism (SNP) identification (Jin et al., 2016; The Aquaculture Genomics, Genetics and Breeding Workshop et al., 2017; Wang, Montague, et al., 2022). However, despite numerous studies on catfish genomes (Table 1), research in pangasiid catfish remains limited.

Within the pangasiid catfishes, only the draft genome of the striped catfish, *P. hypophthalmus* (Gao et al., 2021; Hai et al., 2022; Kim et al., 2018) is available. The first draft genome of *P. hypophthalmus* was obtained using Illumina Miseq and Hiseq sequencing platforms (Kim et al., 2018) and was about 715.8 Mb with scaffold and contig N50 sizes of 14.28 Mb and 6 kb, respectively (Table 1). The striped catfish genome was predicted to consist of 28,600 protein-coding genes. However, in their study on *P. hypophthalmus*, the genome was based on only the Illumina short read. Chromosome-level genome assembly of the same species has been recently reported (Gao et al., 2021; Hai et al., 2022). Using a combination of Illumina short reads, Nanopore long reads and Hi-C data successfully improved the quality of the chromosome-level genome assembly of the striped catfish (Gao et al., 2021) (Table 1). Based on precise long-read HiFi sequencing data, Hai et al. (2022) reported the genome size to be 788.4 Mb, consisting of 381 scaffolds with an N50 length of 21.8 Mb. This latest assembly has a contig N50 of 14.7 Mb, which is 245- and 4.2-fold better than the previous Illumina (Kim et al., 2018) and Illumina-Nanopore-Hi-C-based versions (Gao et al., 2021), respectively. Such studies represent the groundwork for more in-depth genome research on the pangasiid catfishes.

Transcriptome Resources

It is not always possible to study the whole genome, particularly due to budget constraints. Another useful genomic

Table 1
Current genomic information of catfish species

Species	Common name	Chromosome no. (2n)	Genome assembly		Genome annotation	Sequencing platforms	References
			Genome size (Mb)	Scaffold N50 (Mb)			
<i>Pangasianodon hypophthalmus</i>	Striped catfish	2n = 60	715.80	14.28	28,600	Illumina Miseq and HiSeq	Kim et al. (2018)
			731.70	29.50	18,895	Illumina HiSeq X Ten, Nanopore, and Hi-C	Gao et al. (2021)
			788.40	21.80		Illumina NextSeq, Nanopore, and Hi-C	Hai et al. (2022)
<i>Ictalurus punctatus</i>	Channel catfish	2n = 58	783.00	7.73	26,661	Illumina GAIIx, HiSeq, and PacBio	Liu et al. (2016)
			845.40	7.25	21,556	Illumina HiSeq	X. Chen et al. (2016)
<i>Ictalurus furcatus</i>	Blue catfish	2n = 58	841.86	28.20	30,971	Illumina NovaSeq and PacBio	Wang, Su, et al. (2022)
<i>Silurus meridionalis</i>	Southern catfish	2n = 58	738.90	28.04	22,965	Illumina HiSeq X Ten, Nanopore, and Hi-C	Zheng et al. (2021)
<i>Bagarius yarrelli</i>	Giant devil catfish	2n = 56	571.00	3.10	19,027	Illumina HiSeq X Ten and PacBio	Jiang et al. (2019)
<i>Clarias batrachus</i>	Walking catfish	2n = 104	821.80	0.36	22,914	Illumina HiSeq	Li et al. (2018)

approach is the use of transcriptome analysis. It involves studying the complete RNA transcripts produced by the genome in a specific cell, tissue, or organism at a particular developmental stage or under certain conditions (Chu & Corey, 2012; Liu, 2007; The Aquaculture Genomics, Genetics and Breeding Workshop et al., 2017). RNA sequencing, often known as RNA-Seq, is a method that involves sequencing RNA using next-generation sequencing technology (Chu & Corey, 2012). This molecular analysis is crucial in catfish research since it enables researchers to comprehend and compare expression patterns among different genes and investigate the molecular mechanisms that govern diverse biological activities at a given time and condition. A considerable number of transcriptome studies have been done on several catfish species. A few notable ones in various catfish species are described here.

An accurate and complete transcriptome assembly was produced using deep sequencing on several tissues of channel catfish (*I. punctatus*) (Jin et al., 2016; Liu et al., 2016). Based on a high-quality reference genome sequence for *I. punctatus* (Table 1), Liu et al. (2016) successfully assembled transcriptomes from the skin of scaled and scaleless *I. punctatus* catfish to examine differentially expressed genes during scale regeneration. The genomic and transcriptomic data during scale regeneration permitted comprehensive analysis of the genomic basis of the most apparent physical trait of catfish — the evolutionary loss of scales. They found that the loss observed in

scaleless is due to a deficiency in secretory calcium-binding phosphoproteins (SCPP) genes. According to Wang, Montague, et al. (2022), transcriptome analysis reveals that the blue catfish, *I. furcatus* sperm, undergo significant changes in gene expression during cryopreservation. Their RNA-sequencing analysis revealed 849 genes that were upregulated following cryopreservation. These genes include members from all five mitochondrial electron transport chain complexes, indicating an enhancement in oxidative phosphorylation processes. This results in the excessive generation of reactive oxygen species (ROS), which are linked to cell death (Wang, Montague, et al., 2022).

Transcriptome research is also frequently carried out to elucidate the gene expression patterns under various conditions, such as disease resistance. For example, Ruan et al. (2022) identified the pivotal genes in immune response. It elucidated the gene regulatory network of *P. hypophthalmus* when infected with *Aeromonas hydrophila*, an emerging bacterial disease in aquaculture. Their findings show the impact of *A. hydrophila* infection on *P. hypophthalmus* at the transcriptome level, specifically at 0, 4, 12, 24, 36, and 48 hr. It allowed the identification of differentially expressed genes (DEGs) between each major infection period (4, 12, and 24 hr). The infection of *P. hypophthalmus* influences the expression of genes involved in the immune system, influencing numerous biological processes (Ruan et al., 2022). Understanding disease pathogens aids in the development of more

effective medicines, vaccinations, and management techniques to combat this specific disease (Lu & Luo, 2020; Yue & Wang, 2017). With such information, the vast body of research on transcriptome sequencing in catfish production will increase our understanding of the species, refine our methods, and ensure the long-term viability of this aquaculture industry.

Linkage Mapping, Quantitative Trait Loci (QTL), and Marker-Assisted Selection (MAS)

Traditional selective breeding procedures such as selection, crossbreeding, and hybridisation remain the major genetic approaches to improve aquaculture production. However, advances in genomics have led to more advanced techniques of QTL and MAS. QTL mapping, in particular for MAS, was initiated for effective and accurate selection at the turn of the century (Liu, 2003; Liu & Cordes, 2004; Ozaki et al., 2017; Yue, 2014). A linkage map is an ordered sequence of genetic markers positioned along the whole of the chromosomes in the genome. The construction of a linkage map involves four key components: polymorphic markers, genotyping tools, reference families, and software for analysing the linkage between pairwise markers and among markers (Liu & Cordes, 2004; Ozaki et al., 2017; Yue, 2014). QTL and MAS are important concepts in genetics and breeding.

Research in aquaculture improvement has mostly focused on the more economically important traits, including disease resistance,

growth rate, fillet yield, and tolerance to environmental stressors like temperature fluctuations or low oxygen levels (Yue, 2014). QTLs have been identified and mapped in a number of aquaculture species: tilapia (*Oreochromis* spp.), Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*), yellowtail amberjack, *Seriola quinqueradiata*, Japanese flounder (*Paralichthys olivaceus*), giant tiger prawn (*Penaeus monodon*), kuruma prawn (*Penaeus japonicus*), Pacific white shrimp, *Litopenaeus vannamei*, as well as Pacific oyster, *Crassostrea gigas* (Lu & Luo, 2020; Ozaki et al., 2017; The Aquaculture Genomics, Genetics and Breeding Workshop et al., 2017; Yue & Wang, 2017; Yue, 2014). Researchers have used QTL mapping techniques to identify regions of the catfish genome associated with these traits, such as head size, weight, hypoxia tolerance, heat stress or disease resistance that are important to breeders for genetic improvement (Liu & Cordes, 2004; Yue, 2014). However, in catfish, previous studies had mainly focused on the Channel catfish, *I. punctatus* and blue catfish, *I. furcatus* (Jin et al., 2016; Liu, 2003; The Aquaculture Genomics, Genetics and Breeding Workshop et al., 2017).

To implement MAS, DNA is tightly linked to QTL for the traits of interest that need to be identified, as determined by QTL mapping or association studies (Ozaki et al., 2017; Yue, 2014). By identifying these markers, breeders can more efficiently select for desired traits in breeding populations. Traits with low inheritance, late in-development expression, or difficulty

in measuring are ideal candidates for improvement through MAS (Yue, 2014). These findings of traits offer a solid foundation for exploring QTL within breeding populations. Though MAS has been applied in fish aquaculture breeding programmes (Ozaki et al., 2017), there has been little investigation on QTL and MAS in pangasiid catfishes up to this point.

Phylogenetics, Population Genetics, and Mitogenomics

Since the late 1990s, a multitude of phylogenetic analyses of the Pangasiidae family have been conducted. The first molecular phylogenetic study among pangasiid catfish species was conducted by Pouyaud et al. (1998) using 23 enzyme loci on 18 genera of *Pangasius* and *Helicophagus* species. Their study followed a systematic revision of the Asian catfish family Pangasiidae (Roberts & Vidthayanon, 1991) based on morphological characters of specimen types and other materials of pangasiid fishes on 39 nominal species/subspecies. Their study effectively addressed the systematics and phylogenetic relationships of this group. Pouyaud et al. (2000) further expanded their phylogenetic studies on the family Pangasiidae based on combined allozyme data and partial mitochondrial cytochrome *b* gene sequences, with two additional species (20 species). Three monophyletic groups were observed: Group 1 was composed of *P. hypophthalmus* and *P. gigas*, Group 2 was composed of *H. waandersii* and *Helicophagus typus*, and Group 3 was composed of *P. lithostoma*,

Pangasius nieuwenhuisii, *P. humeralis*, *P. kinabatanganensis*, *Pangasius* sp. nov. 1 (*Pangasius kunyit*), *P. krempfi*, *P. larnaudii*, *P. conchophilus*, *P. nasutus*, *Pangasius djambal*, *P. bocourti*, *Pangasius* sp. nov. 2, *P. sanitwongsei*, *Pangasius pangasius*, *P. macronema*, and *P. polyuranodon*. However, phylogenetic relationships within Group 3 were not resolved at the internal nodes (Pouyaud et al., 2000). Although a few pairs of closely related species could be demonstrated, the poor resolution of most internal nodes impeded the full resolution of the phylogeny. Their results were congruent with the previous taxonomic hypothesis of the genus *Pangasius* (Pouyaud et al., 1998; Roberts & Vidthayanon, 1991).

Pouyaud et al. (2004) re-analysed the phylogenetic relationships within the family Pangasiidae using mitochondrial 12S rDNA gene sequences to re-affirm their earlier findings. Four genera, i.e., *Pteropangasius* (accepted name: *Pseudolais*), *Helicophagus*, *Pangasianodon*, and *Pangasius*, were identified using a molecular clock or evolutionary calibration based on two mitochondrial DNA genes (12s rDNA and cytochrome *b*). *Pangasius* was found to be the most derived genus. The analysis hypothesised a divergence time of 7-11 mya for the four pangasiid genera and a second episode of speciation characterised by explosive radiation around 5-8 mya for the genus *Pangasius* (Pouyaud et al., 2004). Phylogenetic reconstructions of the family Pangasiidae based on 16S rRNA and cytochrome oxidase subunit 1 (COI) genes could not fully resolve the relationships of several species in the family (Baharuddin,

2016). However, they were sufficiently efficient for the resolution of the investigated species into four pangasiid genera. A recent mitogenomic study by Abdul Halim et al. (2023) revealed that *P. nasutus* and *P. conchophilus* are sister species with high support (BP: 100%). However, the genetic distance between both was very low at 0.6%, which calls for further investigation. It highlights the contentious phylogenetics and evolutionary relationships of the family Pangasiidae, as genetic distances between several species pairs are comparable to conspecific levels (Duong, Nguyen, et al., 2023; Sriphairoj et al., 2018). The efficacy of COI-based DNA barcoding in discriminating between native and invasive species from the family Pangasiidae in the Pahang River, Malaysia, has also been documented (Baharuddin et al., 2023).

The selection of appropriate and effective molecular markers based on function (protein-coding vs non-coding vs structural RNA) or genomic type (e.g., mitochondrial vs nuclear) is essential for achieving research goals such as a precise phylogenetic reconstruction and species identification (Jamaluddin, 2017). Incorporating mitochondrial and nuclear DNA allows researchers to investigate the impact of incomplete lineage sorting or gene introgression on species delineation in greater depth (Jamaluddin, 2017). Because of their higher mutation rates, mitochondrial DNA genes are more effective in resolving terminal taxa, whereas nuclear DNA genes are well conserved, allowing them to provide deeper taxonomic indications (Miya et al., 2003; Satoh et al., 2016). Karinthanyakit

and Jondeung (2012) combined complete mitochondrial cytochrome b (*cyt b*), 12S rRNA, tRNA-Val, and 16S rRNA and partial nuclear recombination-activating gene 1 (*rag1*) to reconstruct the molecular phylogenies of Thai pangasiid and schilbid catfishes. Four significant clades were discovered within the family Pangasiidae, synonymous with the four genera based on mitochondrial cytochrome b: *Pangasius*, *Pseudolais*, *Helicophagus*, and *Pangasianodon* (Karinthanyakit & Jondeung, 2012). However, the concatenated analyses showed a marked improvement over the single-locus studies in terms of resolution, the number of well-supported nodes, and the accuracy with which the phylogeny of closely related species was estimated.

The first genetic data applying microsatellite markers in pangasiid was reported by Volckaert et al. (1998). Six loci demonstrated allelic variation in three species of catfishes, i.e., *Clarias gariepinus*, *C. batrachus*, and *P. hypophthalmus*. However, the study only revealed the preliminary genetic structure of wild and farmed populations of the three species. Development of microsatellite markers requires a high initial cost and is time-consuming. The various steps in primer design, testing, and optimising polymerase chain reaction (PCR) conditions are tedious and labour-intensive (Liu, 2007; Liu & Cordes, 2004). Since the pioneering study of Volckaert et al. (1998), developing novel primers and their utilisation have rapidly increased, especially in population genetic studies. Z. S. Hogan and May (2002)

designed 27 primer pairs of microsatellite loci which were tested on five species of pangasiid catfishes (*P. krempfi*, *P. bocourti*, *P. conchophilus*, *P. pleurotaenia*, and *H. waandersii*) from the Mekong River Basin. All 27 loci were polymorphic in at least one species, while 15 were polymorphic in at least three. In another study, 11 microsatellite DNA markers for the critically endangered Mekong giant catfish, *P. gigas*, were designed from captive fishes. These microsatellites were also tested on four closely related species (*P. bocourti*, *P. conchophilus*, *P. larnaudii*, and *P. sanitwongsei*) which successfully cross-amplified, demonstrating the usefulness of these markers for assessing genetic diversity in *P. gigas* and other closely related *Pangasius* species (Ngamsiri et al., 2007). In addition to their extensive usage in population genetics, microsatellite markers have also been widely employed in aquaculture and fisheries research, including investigations of genome mapping, breeding studies for parentage, kinships, and QTL marker development (Liu, 2007; Liu & Cordes, 2004; Ozaki et al., 2017; Yue, 2014).

The utilisation of the whole mitochondrial genome, also referred to as mitogenome, generates reliable and robust data with its abundance of phylogenetically informative sites (Miya et al., 2003; Sam et al., 2021); in recent years, mitogenomic research has gained much importance. The assembly of whole mitogenomes is becoming indispensable for genome evolution studies and for establishing

mtDNA reference databases for biodiversity assessment and monitoring (Miya et al., 2003; Sato et al., 2018; Satoh et al., 2016). The last 10 years have seen an explosion of mitogenome investigations, which have allowed for a deeper understanding of the evolutionary relationships among various ray-finned fish families (class Actinopterygii) (Satoh et al., 2016). Yet, data on the mitogenomes of pangasiid species is insufficiently explored; only a few species of mitogenomes are available for the pangasiids (Table 2).

Nevertheless, there is still limited documentation on the region's population structure and genetic variation of pangasiid catfishes. To manage productive fisheries, conserve genetic resources and harvest populations of these catfishes sustainably; it is crucial to understand the genetic diversity and structure of the populations. This information is crucial as knowledge of the precise identification and genetic variability is important in selecting genetically rich broodstocks compatible with a systematic aquaculture programme. Moreover, any restocking programmes require the donor and host populations to be genetically compatible and of the same species (through DNA barcoding). Thus, studying the genetic diversity within catfish populations is essential for maintaining and conserving wild and capture populations. Moreover, information on the phylogenetic relationships of the pangasiid group would be very useful in selecting closely related species as potential candidates for a hybridisation programme.

Table 2
Available mitogenomes of pangasiid catfishes

Species	Sizes (bp)	Accession no.	References
<i>Pangasius bocourti</i>	16,522	MN842723	J. Chen et al. (2020)
<i>Pangasius conchophilus</i>	16,470	OQ078744-OQ078745	Abdul Halim et al. (2023)
<i>Pangasius krempfi</i>	16,475	MZ272453	Duong, Pham, et al. (2023)
<i>Pangasius larnaudii</i>	16,471	AP012018	Zhang et al. (2021)
<i>Pangasius mekongensis</i>	16,462	MZ272451	Duong, Pham, et al. (2023)
<i>Pangasius nasutus</i>	16,465	OP901624, OQ078746, OQ078747	Abdul Halim et al. (2023)
<i>Pangasius pangasius</i>	16,472	KX950698	Unpublished
<i>Pangasius sanitwongsei</i>	16,536	MN809630	Wei et al. (2020)
<i>Pangasianodon gigas</i>	16,533	AY762971	Jondeung et al. (2007)
<i>Pangasianodon hypophthalmus</i>	16,522	KC846907	Zhao et al. (2014)

AQUACULTURE AND ECONOMIC SIGNIFICANCE OF THE PANGASIIDS

Aquaculture is the fastest-growing food-production industry in agriculture, with significant potential for increased supply to meet human protein demands. The major cultured species in the family Pangasiidae (catfishes) are *P. hypophthalmus* (striped catfish) (Cacot, 1998; Griffiths et al., n.d.; Legendre, 1998), *P. gigas* (Mekong giant catfish) (Legendre, 1998; Sriphairoj et al., 2007), *P. bocourti* (Basa catfish) (Cacot, 1998; Legendre, 1998), and *P. djambal* (Jambal catfish) (Iswanto & Tahapari, 2014; Legendre et al., 2000). Pangasiid catfishes have various advantageous traits that make them good candidates for aquaculture. They have rapid growth rates, are well adapted to poor water quality habitats and are omnivorous (Cacot, 1998; Griffiths et al., n.d.; Legendre, 1998).

Vietnam is the world's biggest producer of *Pangasius*. Its production was estimated

to be two billion USD a year, accounting for 70 to 80% of global *Pangasius* production, which is exported to more than 126 countries (Gisbert et al., 2022; Griffiths et al., n.d.; Phuong & Oanh, 2010). Vietnam's Mekong Delta is home to centuries of river catfish culture, making it a valuable resource for aquaculture operations (Cacot, 1998; Gisbert et al., 2022; Phuong & Oanh, 2010). In the early 1960s, *P. bocourti* and *P. hypophthalmus*, locally referred to as Basa and Tra fish, were farmed in small cages and ponds, respectively (Cacot, 1998; Griffiths et al., n.d.; Phuong & Oanh, 2010). Both originate from the Mekong River and Chao Phraya River, are fast-growing, omnivorous, air-breathing species, adaptable to low dissolved oxygen levels (Cacot, 1998; Gisbert et al., 2022; Griffiths et al., n.d.; Legendre, 1998), making them highly amenable to aquaculture. In addition, juvenile *P. hypophthalmus*, commonly referred to as "iridescent sharks", is very

popular in the pet trade. Their black bodies exhibit a blue iridescence and a generalised shark form when young (Armbruster, 2011).

Pangasianodon hypophthalmus was introduced into Malaysia, Indonesia, the Philippines, China, Taiwan, Guam, Bangladesh, and India for aquaculture (Griffiths et al., n.d.). It has since been successfully established as a successful feral species in the introduced waters. For instance, it was first brought into Malaysia from Thailand in the 1980s and was successfully produced in captivity by induced spawning, overcoming supply limitations of fingerlings (Cacot, 1998; Griffiths et al., n.d.; Mohamed Yusoff et al., 2019). Currently, the pangasiid captive catfish are cultured in floating cages along the Pahang River, from Kuala Tembeling to Kuala Pahang. Although the Pahang River is home to three indigenous species: *H. waandersii* (Patin Muncung), *P. micronemus* (Patin Lawang/Juara), and *P. nasutus* (Patin Buah), the introduced species, *Pangasianodon hypophthalmus*, popularly known as ‘Patin Sangkar’, is Malaysia’s most widely cultivated catfish species (Baharuddin, 2016; Hassan et al., 2011; Mohamed Yusoff et al., 2019). In addition to the major cultured pangasiid species mentioned above, other potential aquaculture candidates are *P. nasutus* and *P. krempfi*.

***Pangasius nasutus*: A Rising Aquaculture Species**

In recent years, there has been growing interest in the culture of the native ‘Patin

Buah’, *P. nasutus*, in Peninsular Malaysia and Indonesia. It is a well-known delicacy, but unfortunately, at a market price of > USD 35/kg, it is beyond the budget of most locals (personal communication with local anglers). Furthermore, as the supplies are based on wild capture, these natural resources would be depleted if not strategically managed (Chong et al., 2010; Hassan et al., 2011). A well-structured programme modelled along the lines of the “Catfish Asia” project (Legendre, 1998; Legendre et al., 2000) should be conducted should be followed in other Southeast Asian countries. A culture programme of *P. nasutus* has already been successfully initiated by the Freshwater Fisheries Research Division (FRI Glami-Lemi), Malaysia, through a breeding development programme (Jaapar, 2020) from wild broodstock. The main objective of this facility was to restock the Pahang River as well as several other major rivers in the state of Pahang, which was known to support good numbers before the decline in the last decade (Jaapar, 2020; Jaapar et al., 2021).

A novel fish induction breeding technique was recently introduced in *P. nasutus* (Jaapar, 2020). The procedure involved stimulating mature fishes to reproduce in captivity by introducing pituitary hormones and releasing eggs and sperm from ripe gonads as a result of the stimulation (Jaapar, 2020). Using hormones in the induced breeding of *P. nasutus* enables farmers to produce large quantities of seeds. There are various advantages of using induced breeding to produce seeds:

(1) creates an efficient breeding programme for seed production, (2) allows non-seasonal breeding, (3) produces numerous seeds per induction, (4) allows for the selection of higher-quality parent fish, (5) managing the survival of seeds, and (6) guarantees a lucrative return (Jaapar, 2020). In terms of technical aspects, tagging has also been found to be useful in supporting broodstock management (Jaapar, 2020). The tagging prevents repeated injections of the same fish and inbreeding. This preliminary success could support the freshwater ‘Patin Buah’, *P. nasutus* industry.

The ‘Patin Buah’ has exceptional potential for the food fish export industry with its white-fine-grained and sweet flesh, compared to the yellowish flesh of *P. hypophthalmus* (Hassan et al., 2011; Tahapari et al., 2011). The same characteristics have led to increasing interest in *P. bocourti* (Vietnam) and *P. djambal* (Indonesia) (Iswanto & Tahapari, 2014). Both species are extensively farmed to produce more white-meat catfish in their regions. Hybridisation between *P. nasutus* and other closely related catfish is also being trialled. It is hoped that this would produce hybrids with combined qualities of superior meat and faster growth than the parents (Hassan et al., 2011; Iswanto & Tahapari, 2014; Payseur & Rieseberg, 2016).

***Pangasius krempfi*: Another Rising Aquaculture Species in Coastal Areas**

Unlike most pangasiids, which live in freshwater, *P. krempfi* spends part of its life in brackish and coastal areas along the

Mekong Delta, Vietnam (Duong, Nguyen, et al., 2023; Z. Hogan et al., 2007). Because of its high meat quality and commercial value, it is considered the most expensive catfish (Vu et al., 2020). This species has gained increased interest in aquaculture in the Mekong Delta, Vietnam. However, the domestication process, which started in 2006 (Trinh et al., 2005), has not been fully established. One of the obstacles is the reproductive migratory behaviour of the species, which hinders obtaining a high number of broodstock (Roberts & Baird, 1995; Vu et al., 2020; Z. Hogan et al., 2007). Farmers in the Mekong coastal areas still rely on wild fingerlings for pond culture with some profits (personal communication by farmers in the delta). Admittedly, this is not sustainable, so greater efforts are needed to conserve the species.

Hybridisation and Gene Introgression Among Pangasiid Catfishes

The last few decades have seen increasing research into the evolutionary processes of hybridisation and introgression (the transfer of genes across species-mediated mostly by backcrossing in aquaculture species (Payseur & Rieseberg, 2016; Sriphairoj et al., 2018). Hybridisation is typically employed for genetic improvement by crossbreeding species to outperform either of their parents or combine beneficial traits from both parents.

Interspecific hybridisation between pangasiid species, such as *P. hypophthalmus* X *P. gigas*, *P. hypophthalmus* X *P. bocourti*, and *P. hypophthalmus* X *P. larraudii*, has

been well established mainly in Thailand for their superior characteristics in growth, survival rate, and meat quality (Gisbert et al., 2022; Sripairoj et al., 2018). In addition, hybridisation between *P. hypophthalmus* X *P. nasutus* has also been trialled (Hassan et al., 2011; Iswanto & Tahapari, 2011, 2014; Mohamed Yusoff et al., 2019; Samad et al., 2020; Tahapari et al., 2011). However, Sripairoj et al. (2018) raised concerns about the genetic introgression of these farmed animals into wild populations as interspecific hybridisation among pangasiid species has been known to produce reproductively viable hybrids, such as in the *P. hypophthalmus* X *P. gigas* hybrid. It will be detrimental to the ecological health of the original parents in the habitat when hybrids are superior.

FUTURE PERSPECTIVES

Genomics will likely play a pivotal role in the conservation, breeding, and improvement of pangasiid catfish species. This review briefly describes the current trends in aquaculture, from traditional molecular genetics to NGS genomics approaches in the conservation efforts of the family Pangasiidae catfishes in Southeast Asia. With the rapid advancements in NGS technology and genomic analysis, aquaculture and fisheries management will see a paradigm shift. The following provides an insight into the potential future.

Genomic Sequencing and Annotation

Recent developments in sequencing technology have the potential to greatly improve the speed and cost of whole-

genome sequencing, opening the door to the rapid collection of genomic data for a wide range of catfish species. Furthermore, identifying genes and their roles through genome annotation efforts will yield important insights into features associated with growth, tolerance to illness, and environmental adaptation.

Conservation Efforts

Genomic research permits a comprehensive understanding of the genetic variability, population structure, and adaptation of pangasiid catfish species across numerous environments. This information will greatly aid in identifying and protecting genetically distinct populations and developing successful conservation methods, making it vital for conservation efforts.

Breeding and Improvement

Selective breeding programmes will benefit from using genomic technologies, making it possible to identify desired traits, including disease resistance, growth rate, and stressor tolerance. It will initiate the development of improved strains of pangasiid catfish with higher productivity and resilience. Understanding the genetic basis of disease resistance will enable the development of pangasiid catfish breeds that are more resistant to prevalent diseases, reducing the need for antibiotics and improving overall fish health, as genomic research may focus on identifying genes related to disease resistance in pangasiid catfishes. The beneficial outcome is that the economic losses brought on by diseases in aquaculture

could be effectively addressed. In addition, with the increasing use of MAS and genomic selection approaches, the aquaculture industry will be able to selectively increase certain traits in pangasiid catfish populations.

Market Competition and Demand

It is essential to meet customer demands for high-quality and environmentally friendly seafood. Utilising genomics in catfish aquaculture can enhance farmers' competitiveness by providing higher-quality products.

CONCLUSION

The convergence of aquaculture and genomics in catfish farming has already led to significant advancements in breeding, disease resistance, and overall production efficiency. Continued research and application of genomic knowledge are expected to further revolutionise the catfish industry, making it more sustainable, efficient, and responsive to market demands. Genomic research on pangasiid catfishes is still in its infancy, and currently, only basic data is available on the species investigated, and very few in-depth functional studies have been conducted. The limited fundamental data impedes exhaustive genomic applications in the family Pangasiidae. Nevertheless, the striped catfish (*P. hypophthalmus*) draft genome sequence is already available, and the complete reference genome sequence for the channel catfish (*I. punctatus*) marks an important milestone for structural genomics and functional genomics studies of other species, such as pangasiid catfishes. While

this overview of pangasiid catfishes is not exhaustive, the significant issues highlighted in the published studies are covered. Genomics offers enormous potential in the aquaculture sector and, thus, human well-being.

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