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A review: Status and genetic breeding progress of culters in China

Can Xu [a], Lang Qin [a], Hongxuan Liang [a], Yingying Yang [a], Ming Wen [a], Yuxiang Wang [a], Jinhui Huang [a], Xu Huang [a,b], Fangzhou Hu [a,b], Shi Wang [a,b], Chang Wu [a,b,*]

[a] Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha, China
[b] Yuelushan Laboratory, Changsha, China

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ABSTRACT

The term of culters collectively designates ichthyofauna comprising over ten piscine taxa within the subfamily Culterinae, family Cyprinidae, order Cypriniformes. In recent decades, aquaculture production of culters in China has exhibited a considerable surge, establishing them among the economically significant ichthyofauna in continental freshwater ecosystems. This review synthesizes current knowledge on extensively studied culters, spanning the genera *Culter*, *Ancherythroculter*, and *Chanodichthys*, including their biogeographical distributions and biological traits. Additionally, the advancements at molecular and genomic levels were comprehensively delineated, and the current progress in genetic breeding of culters — specifically distant hybridization, sex-controlled, and molecular-assisted breeding — was elucidated. Finally, the development problems and suggestions for the culters industry were raised. This study provides important foundations for the genetic breeding and industrial development of culters.

In the taxonomic classification, genera such as *Culter*, *Ancherythroculter*, and *Chanodichthys* belong to the Culterinae subfamily within the Cyprinidae family of Cypriniformes. While *Culter* and *Chanodichthys* exclusively inhabit East Asia (China, Vietnam, Korea, and Russia), *Ancherythroculter* is endemic to China [1]. These species constitute a primary freshwater fish group in the Cultrinae subfamily (Cyprinidae), distinguished by their delicate, alabaster flesh, unblemished, non-piscine savor, and substantial nutritional value [2]. Over recent decades, propelled by advancements in aquaculture methodologies and escalating market demands, their cultivation yields have exhibited remarkable augmentation, establishing them as crucial economic species within China's inland natural waterways.

Regrettably, compounding pressures from overexploitation, environmental contamination, and habitat degradation have precipitated precipitous population depletion [3–5]. Overall resource abundance has markedly diminished, with demographic traits trending toward younger cohorts and diminished body dimensions, manifestations demanding urgent remediation [6]. Genetic diversity serves as the intrinsic foundation for fishery enhancement in aquaculture contexts [7]. Consequently, protecting and utilizing the genetic diversity of culter populations has emerged as a paramount priority, engendering extensive investigations into germplasm resources and genetic breeding.

Contemporary research has pursued comprehensive cytogenetic, molecular population genetics, and genomic inquiries concerning culters. Parallel efforts in genetic breeding have yielded superlative new varieties in China, such as "Xianfeng No. 1" and "All-Female No. 1", substantially incentivizing industry progression. With the refinement and expanded deployment of artificial propagation and genetic refinement techniques, the provision of premium culter varieties continues to proliferate, profoundly influencing aquaculture, capture fisheries, and regional economic advancement. Therefore, deepening cognizance of germplasm resource distribution and intensifying genetic breeding research will foster effective preservation and sustainable utilization. This approach facilitates the cultivation of superior strains endowed with exquisite texture, robust resilience, and optimal growth trajectories, thereby elevating aquacultural profitability and ensuring the robust, sustainable evolution of the culter industry.

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* Corresponding author. Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha, 410081, China.
E-mail address: wuchang@hunnu.edu.cn (C. Wu).

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1. Taxonomic classification

Scholars globally have widely pursued taxonomic investigations of culters over preceding decades. In 1855, Basilewsky initially documented six specimens from northern China, founding the genus *Culter* (though without designating a type species). This omission was later rectified by Bleeker, who formally established *Culter alburnus* (topmouth culter) as the genus's type species [8]. In 1909, Berg distinguished species with incomplete ventral keels from *Culter*, establishing the genus *Erythroculter* with *Erythroculter erythropterus* (redfin culter) as its type species. The presence or absence of a fully developed abdominal ventral keel serves as the principal diagnostic characteristic for generic delineation within the Cultrinae subfamily. Subsequently, Yi elucidated the morphological attributes of *Culter* and *Erythroculter*, while resolving cases of synonymy and homonymy [9]. In 1964, Yi and Wu formally instituted the genus *Ancherythroculter*, primarily based on a unique morphological apomorphy, absence of the swim bladder's third chamber, effectively distinguishing it from related genera. Following taxonomic revisions, Luo postulates that species with incomplete ventral keels (historically classified as *Erythroculter*) should be reassigned to *Culter*, while those with complete keels (historically classified as *Culter*) fall under *Chanodichthys*. Applying this criterion, Luo classified the group into 2 genera comprising 11 species and subspecies — a framework garnering broad acceptance [8]. Contemporary research defines culters as encompassing species across multiple Culterinae genera: *C. alburnus*, *C. recurviceps*, *C. mongolicus*, *C. m. elongates*, *C. m. qionghaiensis*, *C. dabryi*, *C. d. shikainensis*, *C. abramoides*, and *C. oxycephaloides* (genus *Culter*); *Ancherythroculter kurematsui*, *A. wangi*, *A. nigrocauda*, and *A. lini* (genus *Ancherythroculter*); *Chanodichthys erythropterus* and *C. compressocorpus* (genus *Chanodichthys*). Presently, extensively studied species include *C. alburnus*, *C. mongolicus*, *C. dabryi*, and *C. oxycephaloides* (*Culter*); *A. nigrocauda* (*Ancherythroculter*); and *C. erythropterus* (*Chanodichthys*).

Conventional culter taxonomy primarily employs external morphological characteristics, such as body configuration, fin architecture, and scale patterning. Traditional classification clusters species like *C. alburnus*, *C. mongolicus*, and *C. dabryi* together, segregates *A. nigrocauda* and *A. lini* as a distinct clade, and isolates *C. erythropterus* as a separate lineage. The mitochondrial *COI* gene, a foundational DNA barcode for species identification, has achieved global adoption for delimiting plant and animal taxa with exceptional precision [10]. Notably, research confirms that *COI* sequences unambiguously differentiate *C. alburnus*, *C. dabryi*, *C. mongolicus*, and *C. oxygastroides* [11]. This study employs *COI* markers for preliminary molecular-level phylogenetic reconstruction of culter species. However, our mitochondrial phylogeny reveals regional populations of *C. mongolicus*, *C. dabryi*, *A. nigrocauda*, and *C. erythropterus* forming non-monophyletic assemblages (Fig. 1), exposing significant limitations in morphology-based classification. Morphological traits prove susceptible to ontogenetic variation and environmental plasticity, potentially perpetuating synonymization errors. Compounding this issue, interspecific phenotypic distinctions among congeneric species exhibit extreme subtlety, precluding reliable differentiation based exclusively on external anatomy.

2. Distribution and biological characteristics

The genera *Culter* and *Chanodichthys* are endemic to East Asia, occurring across China, Vietnam, Korea, and Russia. Within China, their constituent species exhibit expansive distributions throughout rivers, lakes, and reservoirs — excluding the Qinghai-Tibetan Plateau and Xinjiang — extending northward to the Heilongjiang River Basin and southward to Yunnan's inland waters, with principal habitats centered

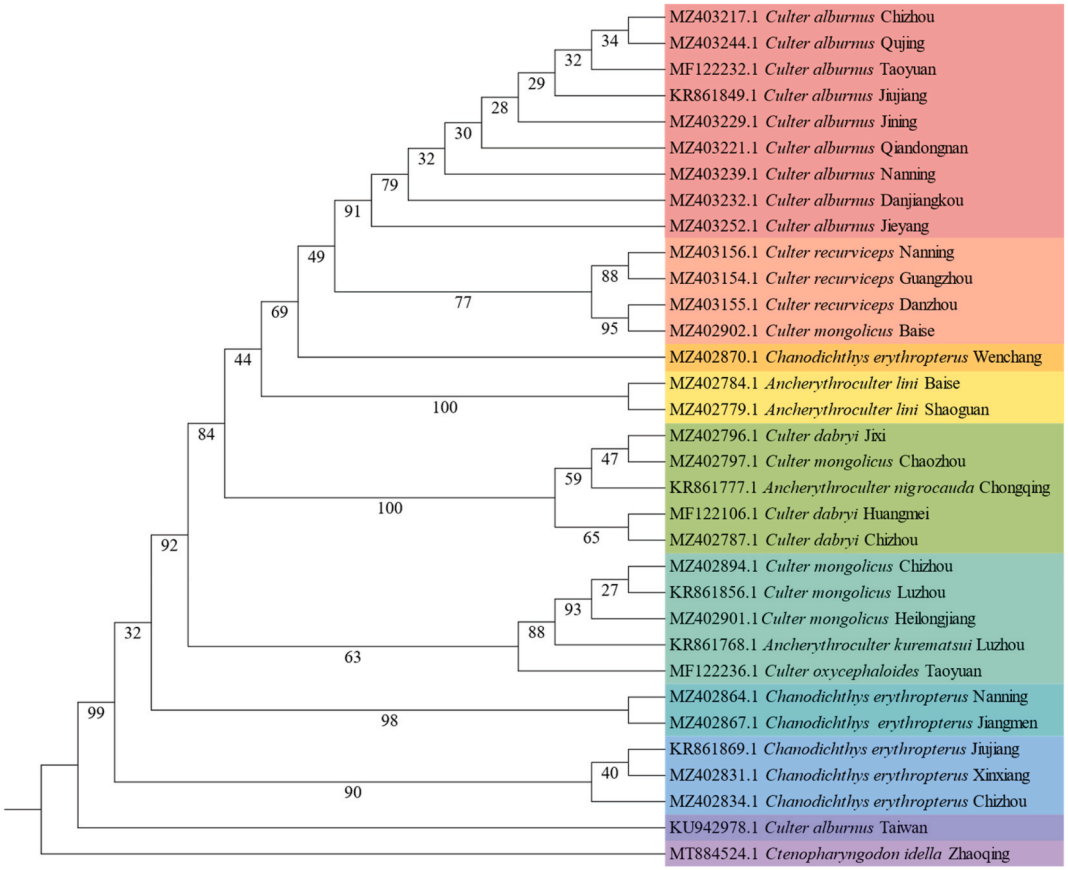

Fig. 1. Phylogenetic tree of culters constructed based on the mtDNA *COI* gene.

in the Yangtze and Pearl River systems [12,13]. *Ancherythroculter*, uniquely endemic to China, concentrates predominantly in Sichuan Province's upper Yangtze tributaries. Nonetheless, profound disparities exist in the distributional ranges across species. *C. alburnus*, for instance, boasts an extensive presence across Taiwan Province and the Pearl, Yangtze, and Heilongjiang River basins, representing a cornerstone of China's freshwater fisheries [14]. *C. recurviceps* remains restricted to Hainan Island's river networks and the Pearl River Basin, where it is esteemed as a prized regional food fish [15]. The Mongolian red culter (*C. mongolicus*) demonstrates a broad transnational range encompassing the Amur and Yangtze Rivers in China and Mongolia's Onon-Kherlen system [16]. Similarly, *C. dabryi* inhabits major drainage basins, including the Minjiang, Qiantang, Yangtze, Yellow, and Heilongjiang rivers [17]. Conversely, *A. nigrocauda* is exclusively endemic to the upper Yangtze [18].

Culters display exceptional growth rates with significant interspecific size variation: *C. alburnus* achieves weights exceeding 10–15 kg (commonly 2–2.5 kg) [19]; *C. mongolicus* similarly attains substantial proportions, while *C. dabryi* (a medium-sized carnivore) generally reaches a total length $\leq$ 35 cm [20]; *C. erythropterus* ranks among the smaller cyprinids [21]; and *A. nigrocauda* may reach 50 cm and 1.5 kg [22]. Distinct ontogenetic habitat shifts occur: adults occupy flowing waters' mid-to-upper strata, whereas juveniles form shallow-water schools — an adaptation mitigating predation threats and current exposure [23]. Behaviorally, these fish exhibit exceptional agility, irascibility, and leaping prowess, though they remain notably timid. Their carnivorous diets transition seasonally: juveniles consume plankton and algae; adults prey predominantly on fish and crustaceans [24].

Ecologically resilient, culters endure temperatures of 0–36 °C, with optimal biological parameters occurring within narrow ranges: 18–26 °C for metabolism, 20–25 °C for growth, and 22–26 °C for reproduction. Temperature critically governs early development: sub-23 °C incubation risks *Saprolegnia* infection, while $>$ 29 °C yields reduced hatch rates and deformed fry [25]. Reproductive phenology typically spans early May to mid-July, modulated by water temperature, flow, and elevation, occasionally extending boundaries to late April or early August [26]. Culter species exhibit significant variation in egg adhesiveness across populations. The eggs of *C. alburnus* demonstrate notable intraspecific variation: Khanka Lake populations produce semi-buoyant, non-adhesive eggs; Yangtze River populations deposit semi-adhesive eggs; while Taihu Lake populations yield adhesive eggs. Similarly, *C. recurviceps* consistently produces adhesive eggs. Among other species, *C. mongolicus* in Jingpo Lake deposits demersal adhesive eggs, *A. nigrocauda* exhibits glutinous adhesion, and *C. erythropterus* likewise develops adhesive eggs [27–31]. Culinarily, culters are celebrated for their alabaster, delicately textured flesh (devoid of piscine flavor) and exceptional nutritional composition: rich in proteins, essential amino acids, and cardioprotective unsaturated fatty acids (notably EPA and DHA), conferring both gastronomic and commercial distinction [32].

3. Research status of germplasm resources

3.1. Studies on morphology

Culters possess an elongated, laterally compressed body featuring a scaleless ventral keel along the abdomen, extending variably from either the pectoral fin base or pelvic fin origin to the anus. The terminal to superior mouth lacks barbels and displays simple labial morphology, with an interrupted postlabial groove and commissural connection between upper and lower lips. Laterally positioned eyes accompany distinctive cranial osteology: a diminutive supraorbital bone and a distantly positioned fifth infraorbital bone that obliquely traverses the posterior margin of the fourth infraorbital bone, angled posterodorsally. A pronounced gap separates the supraorbital and fourth infraorbital bones. Modestly sized, thin scales demonstrate high deciduousness. The complete lateral line follows one of two trajectories: either forming a pronounced arc or descending behind the head, inflecting sharply ventral to the abdomen at the pectoral fin tip, then ascending anterior to the anal fin base before traversing the caudal peduncle midline. The dorsal fin comprises 3 unbranched and 7 branched rays; the anal fin typically exhibits an elongate base with 3 unbranched and 7–35 branched rays. The anus situates immediately anterior to the anal fin origin. Branchial apparatus features variable development, with generally robust gill rakers (some abbreviated) and predominantly triserial pharyngeal teeth. The swim bladder consists of bi- or tripartite chambers terminating in either obtuse or acute posterior margins [1,33]. Herein are detailed the morphological characteristics of some culters:

C. alburnus exhibits a distinctly elongated, laterally compressed body distinguished by a complete ventral keel. Its head displays lateral compression with a dorsally straight profile, terminating in a superior mouth featuring a vertical gape; the robust, upturned lower jaw projects anteriorly beyond the upper jaw — a predatory adaptation. Large eyes occupy the dorsolateral cranium. Small, deciduous scales cover the body. Fin characteristics: dorsal fin origin posterior to pelvic fin base, with a robust unsegmented spine as the terminal unbranched ray; its origin equidistant to snout tip and caudal base, while anal fin origin lies nearer pelvic base than caudal base; pectoral fins short-acuminate; pelvic fins anteroventral to dorsal fin, shorter than pectorals; caudal fin deeply forked. Coloration: dorsum slate-gray; flanks silvery-white; fins uniformly gray-black. Anatomically, it possesses tricameral swim bladder and triserial pharyngeal teeth [1,34].

C. recurviceps presents an elongated, laterally compressed form (201–428 mm TL) featuring slight postcranial dorsal convexity, incomplete ventral keel, and elongate caudal peduncle. Head with dorsally straight profile, abbreviated blunt snout, vertical-gape superior mouth, robust upturned lower jaw, and prominent lateral eyes. Dorsal fin posterior to pelvic base with unsegmented spinous ray; anal fin margin emarginate; acuminate pectoral fins extending near pelvic origin; pelvic fins shorter than pectorals; caudal fin deeply forked (ventral lobe exceeding dorsal). Scales medium-sized; lateral line anteriorly sinuous, posteriorly linear. Pigmentation: dorsum and flanks grayish-black; ventrum silvery-white; fins pale gray. Gill rakers moderately elongated and dense; pharyngeal bones elongate-narrow, uncinate; pharyngeal teeth subconical with hooked apices; swim bladder tricameral [1].

C. mongolicus displays lateral compression with complete ventral keel. Superior mouth possesses oblique gape; mandible slightly upturned. Eyes dorsolaterally positioned; dorsum mildly convex. Dorsal fin origin nearer snout than caudal base; third dorsal ray spinous. Paired fins: pectorals diminutive; pelvics abbreviated, not reaching anal origin when adpressed; caudal deeply forked with carmine ventral lobe. Overall silvery-gray with xanthic fins [1,35].

C. dabryi features elongated lateral compression, postcephalic dorsal convexity, and incomplete ventral keel. Mouth subterminal, obliquely oriented. Ocular: small eyes positioned dorsolaterally. Dorsal fin spines terminating in robust unsegmented ray, mid-dorsally situated. Anal fin lengthy-based, aspinose; origin nearer pelvic than caudal base. Pectoral fins abbreviate-acuminate, failing to reach pelvic origin; pelvic fins anteroventral to dorsal origin, not extending to anal; caudal deeply forked with acuminate lobes (ventral $>$ dorsal). Chromatic: dorsum and upper flanks fulvous; abdomen argentate; fins gray with margins anthracite [1,36].

A. nigrocauda possesses laterally compressed body, cephalically reduced with dorsal convexity. Superior mouth with oblique commissure extending posteriad to nares; mandible projecting. Eyes large; median lateral line mildly decurved. Dorsal fin spines robust; origin nearer snout than caudal base. Pectorals extended, surpassing pelvic base; pelvic tips nearing anus. Ventral keel incomplete; caudal peduncle stout; caudal fin broad. Dorsum grayish-black; flanks and venter silvery-gray; fins grayish; caudal lobes margined fuscous [1].

C. erythropterus exhibits elongate lateral compression, cephalically

compressed and diminutive, with pronounced dorsal arching. Superior mouth lacking barbels; mandible distinctly upturned. Complete ventral keel. Dorsal fin gray-black with robust spines; paired and anal fins of adults xanthous. Chroma: dorsum gray; venter argentate. Pharyngeal teeth triserial; swim bladder tricameral [1].

3.2. Cytogenetic studies

Cytogenetic research on culters has primarily concentrated on chromosomal characteristics, including chromosome number and karyotype, which hold substantial theoretical and practical importance for the conservation and breeding of their germplasm resources. Numerous karyotypic analyses of *C. alburnus* have been conducted in China, yet significant discrepancies exist among reported findings from different areas. Studies on *C. alburnus* from Guizhou determined a diploid chromosome number of 2n = 48, a karyotypic formula of 2n = 16m + 26sm + 6st (NF = 90), comprising 8 metacentric (m), 13 submetacentric (sm), and 3 subtelocentric (st) chromosome pairs without telocentrics (t) [37]. Conversely, specimens from Dongting Lake exhibited 2n = 48 with karyotype 2n = 18m + 10sm + 18st + 2t (NF = 76) [38], while the southern Dianshan Lake population displayed 2n = 48, 24m + 20sm + 4st (NF = 88). The northern Xingkai Lake population reported 2n = 48, 22m + 26sm (NF = 96) [39]. Early analyses of *C. mongolicus* indicated 2n = 48 and karyotype 2n = 11m + 13sm (NF = 96) [40], while a later study documented 2n = 48, 18m + 18sm + 12st (NF = 42), the latter NF value suggesting methodological inconsistencies [38]. *C. dabryi* demonstrated 2n = 48; 18m + 20sm + 10t (NF = 86) [41]. Li et al.'s systematic cytogenetic examination of four culters confirmed consistent diploidy (2n = 48) with species-specific karyotypic patterns: *C. mongolicus* with 2n = 14m + 28sm + 6st (NF = 90); *C. dabryi* with 2n = 16m + 28sm + 4st (NF = 92); *C. oxygastroides* with 2n = 24m + 24sm + 4st (NF = 92); and *C. erythropterus* with 2n = 16m + 26sm + 6st (NF = 90) [42]. *A. nigrocauda* solely exhibits documentation of 2n = 48; 26m + 18sm + 4st (NF = 92). Despite uniform diploidy (2n = 48) across all studied culters, pronounced karyotypic divergence was observed, potentially attributable to genetic differentiation from prolonged biogeographical isolation or technical artifacts arising from chromosomal preparation protocols and analytical inconsistencies.

Hybrid cytogenetic analyses reveal further complexity. Hybrid progeny of *Megalobrama amblycephala* × *C. alburnus* include diploids (2n = 48; 18m + 22sm + 8st) and triploids (3n = 72; 27m + 33sm + 12st) [43]. The hybrid cultivar "Xianfeng No.1" (♀*C. alburnus* × ♂*A. nigrocauda*) possesses 2n = 48; 28m + 18sm + 2st (NF = 94), maintaining parental ploidy while exhibiting stronger paternal karyotypic resemblance [44]. These cytogenetic insights provide valuable foundations for the theoretical framework and practical deployment of novel hybrid lineages in aquaculture.

3.3. Molecular population genetics research

Genetic diversity encompasses hereditary variations both within and among populations. Clarifying the extant genetic diversity of cultivated strains and the historical impacts of management practices is imperative prior to deploying specific stocks for selective breeding or intraspecific hybridization programs [45].

Advances in molecular biology have facilitated the ubiquitous application of mitochondrial DNA (mtDNA), microsatellites, Random Amplified Polymorphic DNA (RAPD), single nucleotide polymorphisms (SNPs), and amplified fragment length polymorphisms (AFLPs) in evaluating population genetic architecture and identifying germplasm resources. Leveraging these molecular markers, extensive research has elucidated genetic diversity patterns in culters [46]. RAPD analysis of *C. alburnus* culture stocks revealed constrained genetic diversity [47], while AFLP assessment of five wild and one cultured population confirmed allelic paucity in captive-bred cohorts relative to wild conspecifics [48]. SNP genotyping of 60 cultured *C. alburnus* from Anhui Province similarly indicated diminished heterozygosity [49]. Development of 14 polymorphic microsatellites for *C. alburnus* germplasm assessment identified the Xingkai Lake population as genetically depauperate, warranting urgent conservation [32,50–52]. Similarly, 13 novel microsatellites characterized for *C. mongolicus* enable precise population genetic parameterization [53]. Analysis of seven Yangtze basin *C. erythropterus* populations across five microsatellite loci documented both low genetic diversity and pronounced inter-lacustrine divergence [54].

Mitochondrial genomics provides critical foundations for sustainable resource management [18]. Complete mitogenomes have been sequenced for multiple culters including *C. alburnus*, *C. recurviceps*, and *A. nigrocauda* [55–58]. Cytochrome *b* analysis of *C. alburnus* across six Yangtze-Huaihe lakes demonstrated low regional diversity with significant intersystemic divergence [59]. *COI* sequencing of five populations identified Taihu Lake as the genetic diversity hotspot, while Songhua Lake exhibited substantial phylogeographic isolation and elevated intraspecific variation [60]. Counterintuitively, combined microsatellite/mtDNA assessments indicated depressed diversity in wild populations relative to cultured stocks [61]. Yangtze *C. mongolicus* populations displayed moderate diversity with cryptic structuring per *COI* phylogenetics [62]. Mitochondrial control region analysis resolved two biogeographically concordant lineages in both *C. alburnus* and *C. mongolicus* [63]. *C. recurviceps* exhibited minimal diversity but marked population differentiation based on *Cytb/ND2/COI* markers [64]. Temporal analysis of *A. nigrocauda* via *Cytb* and microsatellites confirmed diversity depletion between 2001 and 2016 [65]. Integrated morphometric and mitochondrial *COI*, *COII* and *Cytb* evaluation demonstrated maximal nucleotide diversity in *C. alburnus* and minimal in *C. mongolicus*, with phylogenies supporting a (*C. alburnus* and *C. dabryi*) clade sister to *C. mongolicus* [66,67].

These findings collectively implicate biogeographic isolation, habitat fragmentation, and artificial selection as drivers of genetic erosion. Consequently, implementing seasonal fishing moratoria, ameliorating aquatic pollution, restoring riverine connectivity, and establishing conservation hatcheries are critically recommended [65].

3.4. Genomic research on culters

Significant progress has been achieved in culter genomics. The inaugural genome assembly of *C. alburnus* (GCA_009869775.1, 2019) spanned 1.02 Gb, with contig and scaffold N50 values of 1.40 Mb and 3.67 Mb respectively [68]. Subsequent chromosome-level assembly (GWHBOSX00000000, 2022) yielded a 1.05 Gb genome anchored to 24 chromosomes, featuring a contig N50 of 17.8 Mb [69]. Refinement via HiFi and Hi-C technologies (GCA_040182925.1, 2024) produced a high-quality reference predicting 28,228 protein-coding genes [70]. Chromosome-level assemblies for sexually dimorphic *C. mongolicus* genomes were completed in 2023, with the male (GCA_040802225.1; 1.10 Gb, scaffold N50 = 43 Mb) and female (GCA_040802255.1; 1.09 Gb, scaffold N50 = 42 Mb) genomes revealing 33,581 annotated male genes (88.15% functionally characterized) [71]. *A. nigrocauda*'s 2019 chromosome-scale assembly (GWHAAZV00000000) encompassed 1.04 Gb across 2403 contigs (contig N50 = 3.12 Mb) [72], while *C. erythropterus*'s 2022 reference (GCA_024489055.1) spanned 1.085 Gb with functional annotation for 33,041 genes [73].

These high-resolution genomic resources enable comprehensive germplasm evaluation and establish foundational datasets for advancing conservation initiatives and genetic enhancement programs in culter aquaculture.

4. Research status of genetic breeding in culters

Research on the genetic enhancement of culters predominantly centers on three strategic approaches: hybrid breeding, sex-controlled reproduction, and molecular marker-assisted selection (Table 1).

Table 1
New varieties and new germplasm of culters.

Number	Names	Year	Register number	Category	Parental origin	Breeding institutions	References
1	Xianfeng No.1	2012	GS-02-001-2012	Hybrid breeding	*Culter alburnus* (♀) × *Ancherythroculter nigrocauda* (♂)	Wuhan Institute of Fisheries Sciences; Wuhan Xianfeng Aquatic Products Technology Co., Ltd.	[74]
2	Xianfeng No.2	2018	GS-01-005-2018	Hybrid breeding	*Megalobrama amblycephala* (♀) × *Ancherythroculter nigrocauda* (♂)	Wuhan Academy of Agricultural Sciences	[75,76]
3	Taihu Fangbo	2017	GS-02-001-2017	Hybrid breeding	*Culter alburnus* (♀) × *Megalobrama terminalis* (♂)	Zhejiang Freshwater Fisheries Research Institute	[77,78]
4	Lutai Fangbo	2012	GS-02-002-2012	Hybrid breeding	*Megalobrama amblycephala* (♀) × *Culter alburnus* (♂)	Tianjin Huanxin Aquatic Fine Variety Breeding Farm	[79]
5	Wanjiang No. 1	2020	GS-02-001-2020	Hybrid breeding	Female *Culter alburnus* × male (*Culter alburnus* (♂) × *Megalobrama amblycephala* (♀))	Fisheries Research Institute, Anhui Academy of Agricultural Sciences; Anqing Wanyi Jiniu Aquatic Products Breeding; Shanghai Ocean University	[80]
6	All-Female No. 1	2020	GS-04-002-2020	Sex-controlled reproduction	*Culter alburnus* (♀) × Ultraviolet-inactivated *Cyprinus carpio* sperm	Zhejiang Freshwater Fisheries Research Institute	[81]
7	Hybrid Fangbo-A	2010	New germplasm	Hybrid breeding	*Megalobrama amblycephala* (♀) × *Culter alburnus* (♂)	Hunan Normal University	[43,82,83]
8	Xiangjun culter (hybrid Culter No.1)	2020	New germplasm	Hybrid breeding	Female [(*Megalobrama amblycephala* (♀) × *Culter alburnus* (♂) (♀)) × *Megalobrama amblycephala* (♂)] × male *Culter alburnus*	Hunan Normal University	[84]
9	Hybrid Culter No.2	2025	New germplasm	Hybrid breeding	*Culter alburnus* (♀) × *Culter dabryi* (♂)	Hunan Normal University	[85]
10	Hybrid Culter No.3	2023	New germplasm	Hybrid breeding	*Chanodichthys erythropterus* (♀) × *Culter alburnus* (♂)	Hunan Normal University	[86]
11	Hybrid Fangbo-M	2023	New germplasm	Hybrid breeding	*Megalobrama amblycephala* (♀) × *Culter mongolicus* (♂)	Hunan Normal University	[87]
12	Hybrid Fangbo-D	2025	New germplasm	Hybrid breeding	*Megalobrama amblycephala* (♀) × *Culter dabryi* (♂)	Hunan Normal University	[88]

4.1. Research on distant hybridization of culters

Distant hybridization serves as a cornerstone methodology in aquatic breeding, facilitating the integration and genomic innovation of elite traits through intergeneric or interspecific crosses among culter species. This approach provides transformative pathways for enhancing both the quality and production efficiency of culter aquaculture. While multiple domestic research teams have pursued intergeneric hybridization between female *M. amblycephala* and male *C. alburnus*, our research group has achieved a seminal breakthrough: the successful establishment of a fertile hybrid lineage with stable propagation to the F_6 generation [43,82,83,89]. Furthermore, both males and females across the F_1 to F_6 generations exhibit unimpaired gonadal development, while demonstrating pronounced heterosis in growth performance, feed utilization efficiency, muscle quality, hypoxia tolerance, and disease resistance [90,91]. Through the sequential hybridization of female hybrid progeny with male *M. amblycephala* to establish a maternal line, followed by crossing with male *C. alburnus*, we developed the Xiangjun culter. This cultivar features enhanced body width, reduced intermuscular bone count [84], herbivorous feeding behavior, elevated intestinal cellulase activity, superior xenobiotic detoxification capacity, and enhanced glycolytic plasticity [92]. Subsequently, a stabilized allodiploid lineage of Xiangjun culter F_1–F_2 was established by self-crossing the Xiangjun culter F_1 [93]. In 2025, we pioneered bisexual fertile hybrid culters through reciprocal interspecific hybridization (*C. alburnus* × *C. dabryi*), observing significantly accelerated growth relative to both parental species [85]. Parallel work crossing female *C. erythropterus* with male *C. alburnus* yielded hybrids enriched with human-beneficial unsaturated fatty acids, including arachidonic acid (ARA), docosahexaenoic acid (DHA), and eicosapentaenoic acid (EPA) [86]. Additionally, our 2023 hybridization between female *M. amblycephala* and male *C. mongolicus* produced a diploid hybrid combining growth superiority with herbivory [87], while the 2025 cross between female *M. amblycephala* and male *C. dabryi* generated hybrids exhibiting enhanced growth, complete fertility, and optimized muscle nutritional profiles [88].

The Wuhan Institute of Fisheries Sciences developed the "Xianfeng No.1" hybrid (♀ *C. alburnus* × ♂ *A. nigrocauda*) characterized by rapid growth (23.6%–29.6% faster than *A. nigrocauda* and 100.3%–172.4% faster than *C. alburnus*), strong oxygen tolerance, and a docile temperament [74]. Their follow-up "Xianfeng No.2" (♀ *M. amblycephala* × ♂ *A. nigrocauda*) exhibits genetic stability alongside integrated parental traits including accelerated growth (21.9% faster than *M. amblycephala* and 84.8% faster than *A. nigrocauda*), robust disease resistance, and high environmental stress tolerance [75,76]. Tianjin Huanxin Aquatic Fine Variety Breeding Farm engineered the Lutai-Fangbo (♀ *M. amblycephala* × ♂ *C. alburnus*), noted for rapid growth and strong stress resistance [79]. Furthermore, intergeneric hybrids between female *Megalobrama terminalis* and male *C. alburnus* demonstrated significant growth advantages and reduced intermuscular bones [94], while the cross combination (♀ *C. alburnus* × ♂ *M. terminalis*) produced Taihu Fangbo, distinguished by unique morphology, accelerated growth kinetics, and reduced protein dietary requirements [77,78]. The Fisheries Research Institute of Anhui Academy of Agricultural Sciences created "Wanjiang No.1" by crossing male *C. alburnus* with the female F_1 hybrid (♀ *C. alburnus* × ♂ *M. amblycephala*), yielding a variety with rapid growth (32.6%–40.6% faster than *C. alburnus*), low protein dependence, and heightened stress tolerance [80].

While distant hybrid breeding enables elite trait integration through genetic recombination, with most hybrids exhibiting significant heterosis, the technology faces persistent challenges. These include high hybrid offspring mortality, difficulties in fertility regulation, and unverified long-term genetic stability. Future efforts must prioritize elucidating the genetic and reproductive mechanisms underlying piscine distant hybridization. Concurrently, leveraging modern biotechnologies, particularly marker-assisted selection (MAS), will be essential for optimizing hybridization combinations and breeding protocols, thereby advancing the high-quality development of culter aquaculture.

4.2. Research on sex-controlled breeding in culters

Similar to most cyprinids, culters exhibit pronounced sexual size dimorphism (SSD), characterized by female-biased growth superiority. This phenomenon positions all-female aquaculture as a strategic

approach to enhance yield and economic returns [95]. To address this demand, researchers have pioneered methodologies for establishing monosex populations and optimizing sex ratios for commercial-scale production. Furthermore, as a primitive vertebrate, culter has a complex sex-determination system regulated by both genetic and environmental factors. Elucidating its genetic basis is of great practical value for improving the production performance of farmed culters [75].

For instance, the intercross of gynogenetic *C. alburnus* females with physiologically masculinized conspecific males produced the "All-Female No.1" cultivar, which exhibits uniform growth patterns, accelerated development rates (17.0% faster than *C. alburnus* on average), and typical ovarian differentiation. This study also found that under pond culture conditions, a 15-day pond spray of 1 g/L testosterone propionate combined with a 105-day oral administration of 17α-MT (30 μg/g–60 μg/g–100 μg/g–120 μg/g–140 μg/g) constituted the optimal method for inducing physiologically masculinized males in *C. alburnus*. Most 36-month-old pond-cultured individuals were capable of producing semen [81]. Furthermore, Zhang et al. identified two male-specific molecular markers in "Xianfeng No.2" hybrids and paternal *A. nigrocauda* via 2b-RAD-seq, confirming an XX/XY sex determination system in both taxa. These markers significantly enhance precision in monosex breeding programs [75]. Complementary research elucidated epigenetic regulation through *Sox9* promoter CpG methylation, which modulates sexually dimorphic gene expression in *C. alburnus* [96]. This mechanism advances foundational understanding of sex determination while guiding sex-controlled breeding technology development.

4.3. Research on molecular-assisted breeding of culters

Liu et al. leveraged Genotyping-by-Sequencing (GBS) to sequence *M. terminalis*, *C. alburnus*, *C. mongolicus*, and their hybrid progenies, yielding 97,911 SNP markers. This genomic resource facilitates precise genetic identification of parental species and hybrid lineages [97]. Complementarily, transcriptome data and PCR enabled cloning of the full-length *Runx2b* coding sequence in *C. alburnus*. Spatiotemporal expression analysis revealed coordination between this gene's transcriptional dynamics and juvenile intermuscular bone ossification, functionally implicating *Runx2b* in skeletogenesis and establishing a molecular framework for developing intermuscular bone-free germplasm [98]. Moreover, a highly contiguous *C. alburnus* genome assembly enabled identification of candidate genes and quantitative trait loci (QTLs) underlying sex determination, intermuscular spine number, and body weight variation [99]. A comprehensive transcriptome atlas further revealed 524 immune-related genes distributed across 13 conserved immunological pathways [100]. Regarding environmental adaptation, Chi et al. systematically profiled stress-responsive genes in renal, hepatic, and muscular tissues of *C. alburnus* via Illumina sequencing, providing molecular targets for breeding enhanced stress tolerance [101]. Parallel hypoxia research in *A. nigrocauda* characterized gene expression signatures, alternative splicing events, and cardiocerebral signaling pathways during hypoxic exposure (1.5–4.5 h) and reoxygenation [102].

Collectively, these molecular insights significantly advance precision breeding strategies — supporting germplasm conservation, enabling targeted trait enhancement, and reinforcing theoretical foundations for heterosis exploitation in culter aquaculture. This integrated genomics-to-phenomics approach facilitates evidence-driven development of improved culter varieties.

5. Recommendations and prospects

China's notable achievements in culter germplasm resource utilization and genetic breeding, particularly in distant hybridization and gynogenesis, have yielded superior varieties including "Xianfeng No. 1" and "All-Female No. 1". Analysis of current research reveals critical unresolved challenges while clarifying future developmental priorities. Consequently, this paper proposes targeted strategies to address existing constraints within the culter industry.

Culter's tender-textured flesh signifies significant market potential. Industrial development, however, remains hindered by multiple bottlenecks restricting full economic valuation. The fundamental constraint lies in the species' inherent physiological limitations, notably low hypoxia tolerance and compromised stress resistance. These traits directly suppress aquaculture yields and survival rates while rendering live transport exceptionally challenging. Presently, live culter products occupy minimal market share, with over 80% distributed as ice-chilled commodities. This distribution mode diminishes product value and degrades consumer experience, constituting a critical barrier to industry-wide quality and efficiency enhancement.

Nevertheless, substantial knowledge gaps persist regarding the genetic architecture underlying culters commercially valuable traits. Core genes and molecular regulatory mechanisms governing hypoxia tolerance, stress resilience, growth performance, and other economically pivotal characteristics remain functionally uncharacterized. This critical lacuna obstructs precision breeding initiatives utilizing molecular markers and impedes targeted genetic enhancement programs.

Additionally, the profusion of intramuscular bones substantially curtails culter's culinary appeal, particularly for vulnerable demographics like children and the elderly. Gene editing technology offers a groundbreaking solution: empirical studies confirm that targeted knockout of the *Runx2b* gene effectively eliminates these bones. However, its industrial application faces the following challenges: unvalidated long-term food safety of gene-edited culters due to unaddressed biological or biochemical changes; an incomplete ecological risk assessment system with unclear environmental release impacts on aquatic germplasm and ecosystems; absence of regulatory frameworks, industrialization norms and market access mechanisms blocking the policy channel for transformation achievement.

Culter's premium quality traits, combined with consecutive technological breakthroughs, establish a robust foundation for high-quality industry advancement. Future initiatives should prioritize two focal areas: First, advancing aquaculture system modernization through precision water quality management, smart aeration technologies, and stress-resistant strain development. Systematically improving survival rates and yield per unit area will overcome live transport barriers exacerbated by the species' stress sensitivity. Secondly, intensify fundamental investigations into the genetic foundations of economically vital traits in culters. Expedite the discovery and functional validation of core genes regulating hypoxia tolerance, stress resilience, growth efficiency, and other commercially pivotal characteristics; develop corresponding molecular markers; and implement an integrated genomic selection platform for precision breeding. In addition, accelerating regulatory frameworks for gene editing. Integrating traditional hybridization with modern biotechnology will generate definitive solutions to the century-old bone impediment constraining consumer acceptance. As these technical-industrial bottlenecks are progressively resolved, the culter sector is poised to enter an era of premium-quality sustainable development.

CRediT authorship contribution statement

Can Xu: Writing – original draft. **Lang Qin:** Data curation. **Hongxuan Liang:** Investigation. **Yingying Yang:** Investigation. **Ming Wen:** Software. **Yuxiang Wang:** Investigation. **Jinhui Huang:** Investigation. **Xu Huang:** Writing – review & editing, Supervision, Funding acquisition. **Fangzhou Hu:** Supervision. **Shi Wang:** Supervision. **Chang Wu:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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