

## Article

# Fish Roaming in Paintings: Fish Diversity Depicted in Chinese Paintings from the Song to Qing Dynasties

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## Abstract

Surviving ancient paintings themed on fish constitute a type of documentary source that has not yet been fully exploited in ichthyological research. In this study, 101 Chinese paintings dating back to the Song–Qing dynasties were examined. Fish depicted in these paintings were taxonomically identified, and an Index of Relative Commonness (IRC) was developed to quantify the commonness of each genus-level statistical unit across dynastic painting corpora. Across all artworks, 39 statistical units (including 38 genera and goldfish) belonging to 23 families and 9 orders were identified, with 268 cumulative occurrence counts recorded. At the ordinal, familial, and generic taxonomic ranks, Cypriniformes, Cyprinidae, and *Siniperca* represented the most frequently occurring statistical units, respectively. Based on quantitative IRC analysis, the detected statistical units were classified into four occurrence groups, including 2 common, 14 frequent, 15 occasional, and 8 rare units within paintings. At the dynastic level, 10 Song-dynasty paintings produced 49 valid fish occurrence counts covering 22 statistical units; 15 Yuan-dynasty paintings yielded 52 counts across 23 statistical units; 19 Ming-dynasty paintings generated 77 counts representing 27 statistical units; and 57 Qing-dynasty paintings returned 90 counts for 21 statistical units. Historical shifts in the stylistic traditions of Chinese fish paintings and the influences of these stylistic changes on the taxonomic composition and numerical distribution of depicted fish taxa were further investigated. The results of this study complement textual historical records and offer a new complementary resource for modern research on fish biogeography.

**Keywords:** ancient China; Chinese paintings; fish diversity; historical dynamics



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## 1. Introduction

Reconstructing the historical distribution and community dynamics of organisms using diverse historical documents is a classic approach within historical biogeography. Research drawing on Chinese historical archives has demonstrated substantial range contractions among large mammalian species across China over the past two millennia [1]. Furthermore, by comparing ancient and modern sources and systematically compiling information preserved in historical texts, Chinese and international scholars have clarified historical shifts for a broad range of biological groups. These examples include species turnover among native medicinal plants, evolutionary shifts in reptile assemblages, and distributional changes for the Yangtze finless porpoise [2–4]. Nevertheless, textual historical

records carry inherent limitations: such sources mostly deliver broad descriptions of species persistence and range shifts, lack fine-scale documentation of organismal morphology, and are often fragmented and susceptible to subjective interpretive bias.

Unlike written archives, visual artistic materials preserved across historical periods can deliver finer-grained biological and ecological data and constitute a valuable yet underutilised resource for historical ecological research. Textual sources can only document organismal morphology and distribution in qualitative terms. Moreover, common names for a single species frequently differ across time periods and geographic regions, which complicates modern taxonomic interpretation. In contrast, pictorial artworks can directly preserve morphological diagnostic traits for species identification, thereby mitigating confusion caused by inconsistent nomenclature. A growing body of scholarship validates the scientific reliability of ancient pictorial sources. Case studies illustrate that Song-dynasty Chinese paintings accurately reflect avian diversity from that era [5,6]; quantitative analysis of Dutch still-life oil paintings has reconstructed historical floristic composition and species distributions [7]; and early-modern European oil paintings capture decadal-to-centennial-scale shifts in regional aquatic biodiversity [8].

Fish are key aquatic organisms closely tied to human livelihood and socioeconomic activities. Existing studies of ancient fish fauna largely depend on written historical sources such as local gazetteers and pre-modern agricultural treatises. Through systematic compilation of textual archives, prior work has explored the links between artificial-selection theory and ancient goldfish domestication [9], the co-evolutionary dynamics of Neolithic fish–rice polyculture systems [10], and patterns of human exploitation and consumption of aquatic shellfish and finfish in pre-modern societies [11]. Fish also served as a recurring motif for both court-appointed and literati painters in ancient China. Depictions of fish morphology, behaviour, and habitats in ancient paintings not only record pre-modern human observational understanding of nature, but also partially reflect the cultural importance of different fish taxa across successive historical periods. Furthermore, these ancient paintings hold documentary reference value for modern ichthyological research.

The Chinese paintings spanning the Song through Qing dynasties were selected as research material in this study. Fish imagery in these paintings was identified and systematically compiled to characterise fish diversity recorded in paintings from different historical periods. Temporal variations in genus-level occurrence counts across dynastic paintings were analysed to further explore historical changes in human cultural associations with different fish taxa. This work aims to expand interdisciplinary research perspectives for ancient painting studies and to understand the relationships between artistic creation, natural environments, and historical contexts.

## 2. Materials and Methods

### 2.1. Data Sources

A total of 101 Chinese paintings dating from the Song to the Qing dynasties were assembled for statistical analysis: 10 works from the Song dynasty, 15 from the Yuan dynasty, 19 from the Ming dynasty, and 57 from the Qing dynasty. All paintings were public-domain ancient artworks; digital reproductions were retrieved from the Chinese Treasure Gallery, an online repository for ancient Chinese art. We have verified that no copyright issues apply to these paintings. The selected artworks primarily feature fish-related motifs, including swimming fish, fish among submerged vegetation, and fish within aquatic settings.

## 2.2. Species Identification

Unlike highly precise modern scientific illustrations, ancient paintings are artistic creations, and they rarely provide the quantitative morphological traits required for species-level taxonomic assignment. To ensure identification reliability, taxonomic assignments were restricted exclusively to the genus level, and species-level determinations were not attempted. Fish imagery in paintings was evaluated via expert consensus. The evaluation panel consisted of three to five fish-taxonomy specialists holding doctoral degrees, each with more than ten years of relevant research experience. The identification workflow proceeded as follows. First, three taxonomists performed preliminary assessments for each painted fish figure. When all three experts reached identical genus-level assignments, the genus was accepted directly. If at least one taxonomist proposed an alternative identification, two additional experts were invited to re-evaluate the painted fish image. The identification result was adopted only when more than half of the participating experts reached agreement.

## 2.3. Statistical Analysis

For tallying occurrence data, each fish genus was counted as a single occurrence event per painting. Multiple individuals belonging to the same genus within one painting were counted only once. Fish genera were adopted as the basic statistical unit in this study. Although goldfish are conspecific with wild *Carassius auratus*, goldfish were treated as an independent statistical unit to facilitate analysis of its occurrence patterns across successive historical periods.

Following the conceptual framework of the Index of Relative Importance (IRI) [12], an Index of Relative Commonness (IRC) was developed using painting-derived occurrence counts to quantify the commonness of each statistical unit across dynastic painting corpora. The IRC formula is defined as

$$\text{IRC} = \text{N}\% \times \text{F}\%$$

where N% is the proportion of occurrence counts for each fish genus across all paintings, and F% is the dynastic occurrence ratio, calculated as the number of dynasties in which a given genus was documented divided by the total number of investigated dynasties (fixed value = 4: Song, Yuan, Ming, and Qing).

Adapting classification thresholds published in a prior study [13], statistical units were assigned to four categories:

Common statistical units within paintings:  $\text{IRC} \geq 1000$ ; frequent statistical units within paintings:  $100 \leq \text{IRC} < 1000$ ; occasional statistical units within paintings:  $10 \leq \text{IRC} < 100$ ; rare statistical units within paintings:  $\text{IRC} < 10$ .

All data compilation and statistical processing were completed in Microsoft Excel 2010. Figures were generated using Microsoft Excel (version 2010) and Adobe Photoshop (version CS6). Owing to substantial disparities in fish depiction abundance across dynastic painting groups, only descriptive analyses based on absolute counts were performed.

## 3. Results

Across the 101 surveyed paintings, 39 statistical units (including 38 genera and goldfish) representing 23 families within 9 orders were identified (Table 1). Cypriniformes contained the highest richness, with 17 genera and goldfish, accounting for 46.15% of all identified statistical units. Perciformes ranked second with 8 statistical units (20.51%). Siluriformes and Clupeiformes each contributed 3 statistical units (7.69%). Beloniformes and Acipenseriformes each contained 2 statistical units (5.14%). By contrast, Pleuronectiformes, Myliobatiformes, and Tetraodontiformes exhibited the lowest richness, each represented by a single statistical unit (2.56%) (Figure 1A).

**Table 1.** Names of fish statistical units and their primary taxonomic affiliations.

| Order             | Family           | Genus                       |
|-------------------|------------------|-----------------------------|
| Acipenseriformes  | Acipenseridae    | <i>Acipenser</i>            |
|                   | Psephuridae      | <i>Psephurus</i>            |
| Beloniformes      | Hemiramphidae    | <i>Hyporhamphus</i>         |
|                   | Adrianichthyidae | <i>Oryzias</i>              |
| Clupeiformes      | Engraulidae      | <i>Coilia</i>               |
|                   | Pristigasteridae | <i>Ilisha</i>               |
|                   | Clupeidae        | <i>Konosirus</i>            |
| Cypriniformes     | Cyprinidae       | <i>Hemiculter</i>           |
|                   |                  | <i>Carassius</i>            |
|                   |                  | <i>Carassius</i> (Goldfish) |
|                   |                  | <i>Cyprinus</i>             |
|                   |                  | <i>Ctenopharyngodon</i>     |
|                   |                  | <i>Culter</i>               |
|                   |                  | <i>Rhodeus</i>              |
|                   |                  | <i>Parabramis</i>           |
|                   |                  | <i>Pseudorasbora</i>        |
|                   |                  | <i>Hypophthalmichthys</i>   |
|                   |                  | <i>Misgurnus</i>            |
|                   |                  | <i>Aristichthys</i>         |
|                   |                  | <i>Onychostoma</i>          |
|                   |                  | <i>Acheilognathus</i>       |
|                   |                  | <i>Abbottina</i>            |
|                   |                  | <i>Hemibarbus</i>           |
|                   |                  | <i>Opsariichthys</i>        |
|                   |                  | <i>Myxocyprinus</i>         |
|                   | Catostomidae     | <i>Myxocyprinus</i>         |
| Myliobatiformes   | Dasyatidae       | <i>Dasyatis</i>             |
| Perciformes       | Serranidae       | <i>Siniperca</i>            |
|                   | Osphronemidae    | <i>Macropodus</i>           |
|                   | Odontobutidae    | <i>Odontobutis</i>          |
|                   | Channidae        | <i>Channa</i>               |
|                   | Cottidae         | <i>Trachidermus</i>         |
|                   | Gobiidae         | <i>Acanthogobius</i>        |
|                   | Mastacembelidae  | <i>Sinobdella</i>           |
|                   | Lateolabracidae  | <i>Lateolabrax</i>          |
| Pleuronectiformes | Cynoglossidae    | <i>Cynoglossus</i>          |
| Siluriformes      | Bagridae         | <i>Pelteobagrus</i>         |
|                   |                  | <i>Pseudobagrus</i>         |
| Siluriformes      | Siluridae        | <i>Silurus</i>              |
| Tetraodontiformes | Tetraodontidae   | <i>Takifugu</i>             |

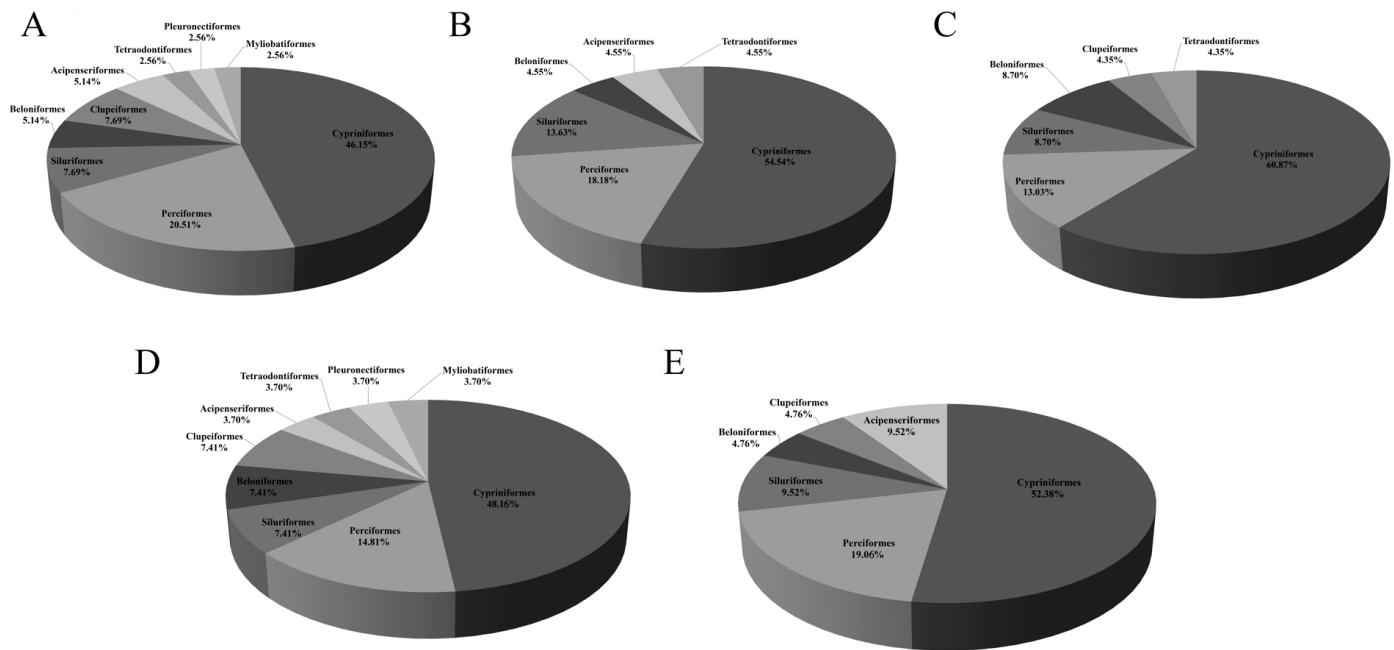


**Figure 1.** Proportional representation of identified statistical units at the ordinal taxonomic rank. (A) Aggregated statistical results across all four dynasties; (B) Song dynasty; (C) Yuan dynasty; (D) Ming dynasty; (E) Qing dynasty.

### 3.1. Distribution of Statistical Units Within Dynastic-Period Paintings

Cypriniformes, Perciformes, and Siluriformes consistently constituted the largest proportions of statistical units represented in paintings across all four dynasties. In Song-dynasty paintings (Figure 1B), proportional richness of statistical units followed the sequence: Cypriniformes (54.54%) > Perciformes (18.18%) > Siluriformes (13.63%) > Beloniformes (4.55%) = Acipenseriformes (4.55%) = Tetraodontiformes (4.55%). Clupeiformes, Pleuronectiformes, and Myliobatiformes were absent (0.00%). For Yuan-dynasty paintings (Figure 1C): Cypriniformes (60.87%) > Perciformes (13.03%) > Siluriformes (8.70%) = Beloniformes (8.70%) > Clupeiformes (4.35%) = Tetraodontiformes (4.35%). Acipenseriformes, Pleuronectiformes, and Myliobatiformes were not documented (0.00%). The sequence for Ming-dynasty paintings (Figure 1D) was as follows: Cypriniformes (48.16%) > Perciformes (14.81%) > Siluriformes (7.41%) = Beloniformes (7.41%) = Clupeiformes (7.41%) > Acipenseriformes (3.70%) = Tetraodontiformes (3.70%) = Pleuronectiformes (3.70%). Only Myliobatiformes was absent (0.00%). For Qing-dynasty paintings, the sequence was as follows (Figure 1E): Cypriniformes (52.38%) > Perciformes (19.06%) > Acipenseriformes (9.52%) = Siluriformes (9.52%) > Beloniformes (4.76%) = Clupeiformes (4.76%). Tetraodontiformes, Pleuronectiformes, and Myliobatiformes had no recorded representations (0.00%).

Figure 2A illustrates genus-level occurrence counts across paintings from all four dynasties. Eleven statistical units were documented in paintings from every dynastic period: *Hemiculter*, *Carassius*, *Siniperca*, *Cyprinus*, *Pelteobagrus*, *Ctenopharyngodon*, *Silurus*, *Culter*, *Rhodeus*, *Parabramis*, and *Oryzias*. In contrast, 11 statistical units appeared exclusively within paintings from a single dynasty. This group included *Trachidermus*, *Acanthogobius*, *Pseudobagrus*, *Ilisha*, *Cynoglossus*, *Konosirus*, *Dasyatis*, *Sinobdella*, *Lateolabrax*, *Myxocyprinus*, as well as goldfish (*Carassius*).

Figure 2B compares 3 metrics across the four dynasties: number of sampled paintings, total occurrence counts of all statistical units, and total number of statistical units. The 10 Song-dynasty paintings contained 49 fish occurrence counts spanning 22 statistical units; *Hemiculter* (count = 6) and *Siniperca* (count = 5) represented the most frequently encountered statistical units. The 15 Yuan-dynasty paintings generated 52 occurrence

counts for 23 statistical units. High-count statistical units for this period were *Carassius* (count = 6), *Siniperca* (count = 6), *Hemiculter* (count = 5), and *Pelteobagrus* (count = 5). The 19 Ming-dynasty paintings yielded 77 occurrence counts across 27 statistical units; *Siniperca* (count = 10) and *Cyprinus* (count = 10) were the most common, followed by *Hemiculter* (count = 6) and *Carassius* (count = 6). Among the 57 Qing dynasty paintings, 90 occurrence counts covering 21 statistical units were recorded. High-count taxa included *Hemiculter* (count = 13), goldfish (*Carassius*, count = 12), *Siniperca* (count = 10), *Cyprinus* (count = 9), *Silurus* (count = 7), *Culter* (count = 7), *Pelteobagrus* (count = 5), and *Trachidermus* (count = 5).

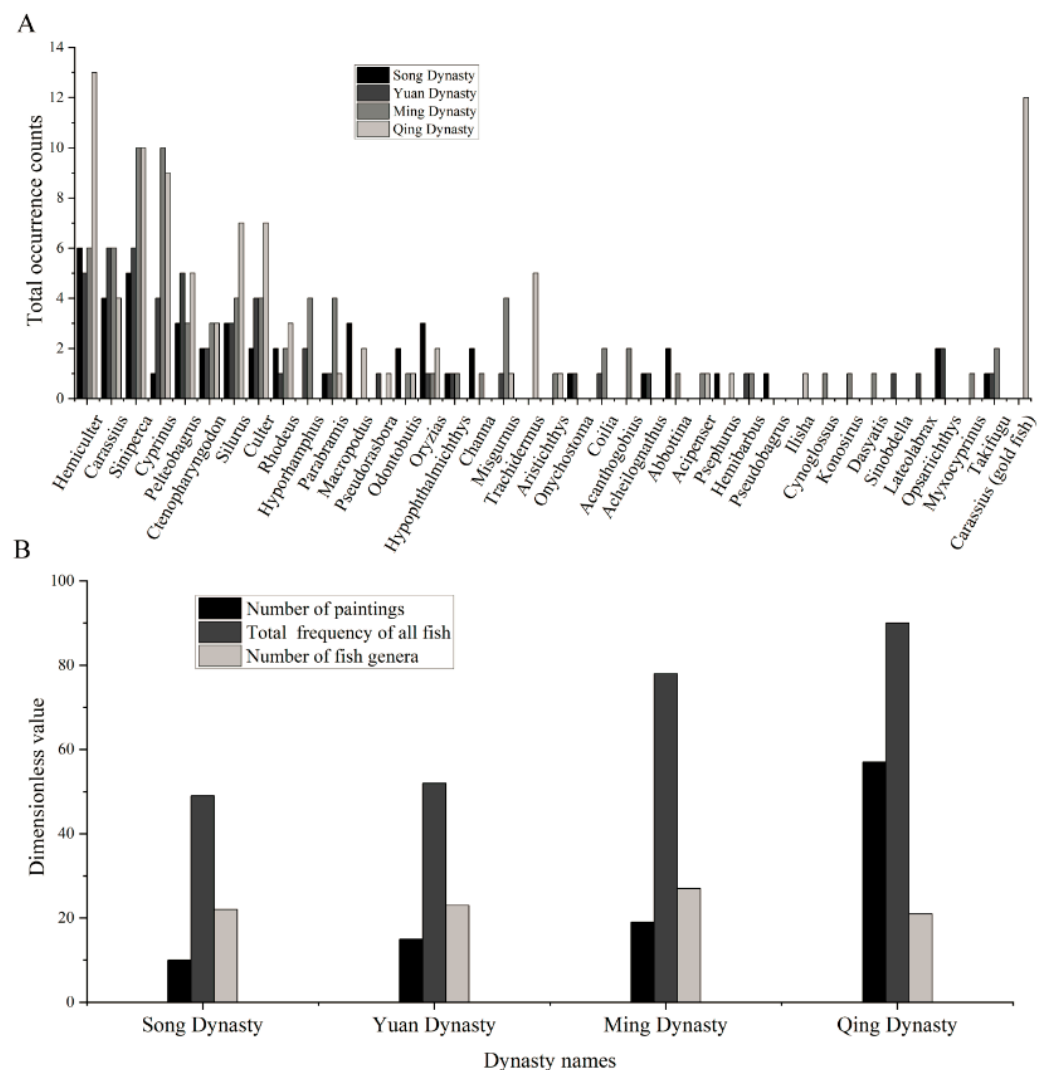


**Figure 2.** Occurrence-count metrics for statistical units across dynastic painting corpora. (A) Genus-level occurrence-count distribution for all statistical units across the four dynasties; (B) Comparative metrics showing the number of sampled paintings, total occurrence counts of all statistical units, and total number of statistical units documented for each dynasty.

### 3.2. Total Occurrence Counts Across Taxonomic Ranks

Cumulative occurrence counts for all statistical units across the full painting corpus totalled 268. At the ordinal rank, statistical units with more than 10 occurrence counts were Cypriniformes (154), Perciformes (52), Siluriformes (34), and Beloniformes (13). Pleuronectiformes and Myliobatiformes exhibited the lowest counts, each documented only once (Figure 3A). At the family rank, Cyprinidae (147), Serranidae (31), Bagridae (17), and Siluridae (17) obtained more than 10 occurrence counts. Families with the fewest records (one occurrence each) were Cynoglossidae, Pristigasteridae, Clupeidae, Dasyatidae, Mas-

tacembelidae, Lateolabracidae, and Catostomidae (Figure 3B). At the analytical unit level, genera with at least 10 occurrence counts, sorted from high to low, were as follows: *Siniperca* (31), *Hemiculter* (30), *Cyprinus* (23), *Carassius* (20), *Silurus* (17), *Culter* (17), *Pelteobagrus* (16), goldfish (12), and *Ctenopharyngodon* (10). The rarest statistical units, each documented once, were *Pseudobagrus*, *Ilisha*, *Cynoglossus*, *Dasyatis*, *Sinobdella*, *Lateolabrax*, *Konosirus*, and *Myxocyprinus* (Figure 3C).

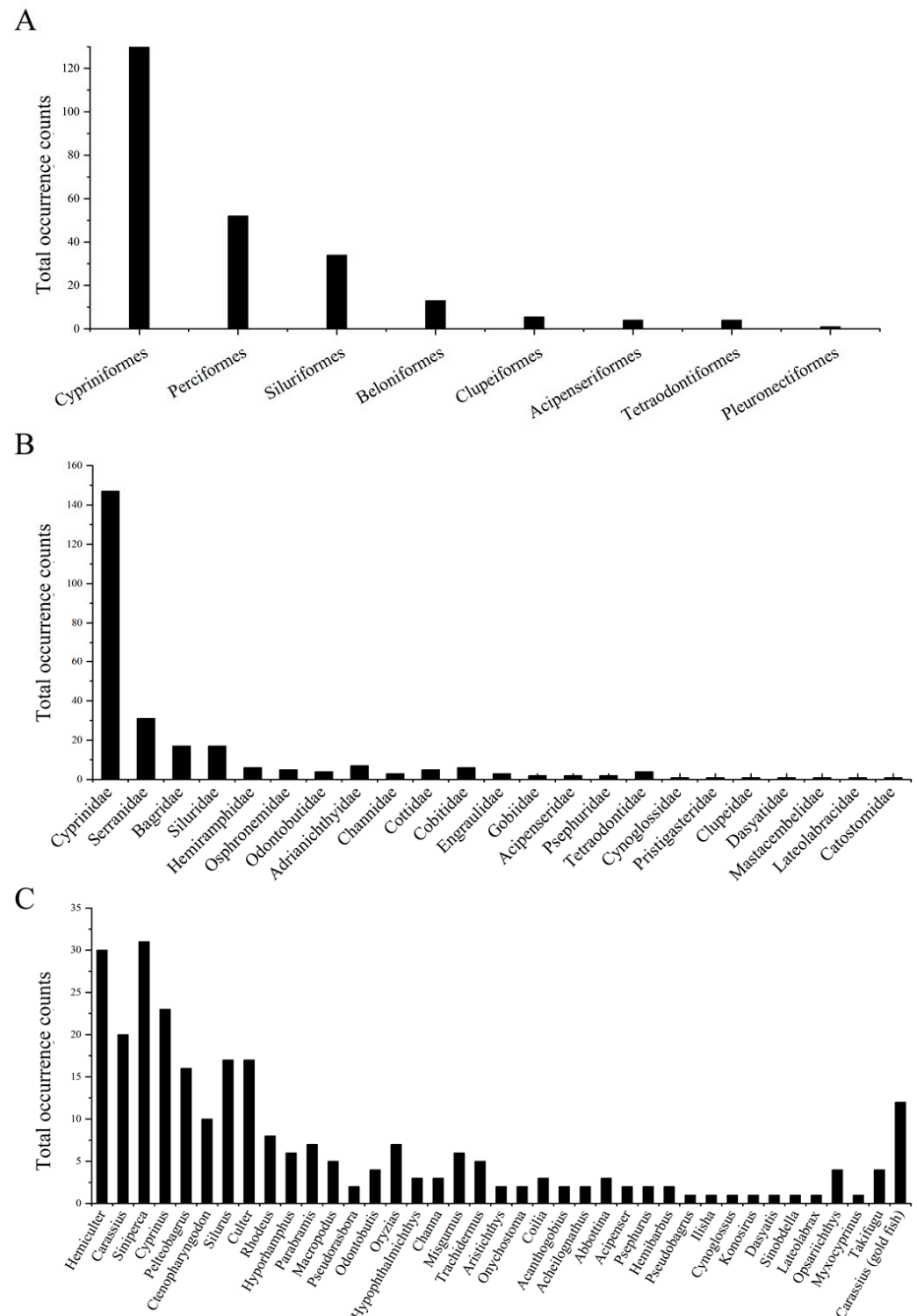


**Figure 3.** Total occurrence counts of identified statistical units aggregated across all paintings: (A) taxonomic order level; (B) family level; (C) genus level.

The values of IRC for all statistical units are presented in Figure 4. Applying our IRC threshold criteria, two common statistical units within paintings were identified: *Siniperca* and *Hemiculter*. Fourteen frequent statistical units within paintings were recognised: *Cyprinus*, *Carassius*, *Silurus*, *Culter*, *Pelteobagrus*, *Ctenopharyngodon*, *Rhodeus*, *Parabramis*, *Oryzias*, *Misgurnus*, *Hyporhamphus*, *Odontobutis*, *Takifugu*, and goldfish (*Carassius*). Fifteen occasional statistical units within paintings were detected: *Macropodus*, *Hypophthalmichthys*, *Opsariichthys*, *Channa*, *Coilia*, *Abbottina*, *Trachidermus*, *Pseudorasbora*, *Aristichthys*, *Onychostoma*, *Acheilognathus*, *Acipenser*, *Psephurus*, *Hemibarbus*, and *Acanthogobius*. Eight rare statistical units within paintings were recorded: *Konosirus*, *Pseudobagrus*, *Ilisha*, *Cynoglossus*, *Dasyatis*, *Sinobdella*, *Lateolabrax*, and *Myxocyprinus*. Across all statistical units within paintings, *Siniperca* yielded the highest IRC (1156.72), followed by *Hemiculter* (1119.40).

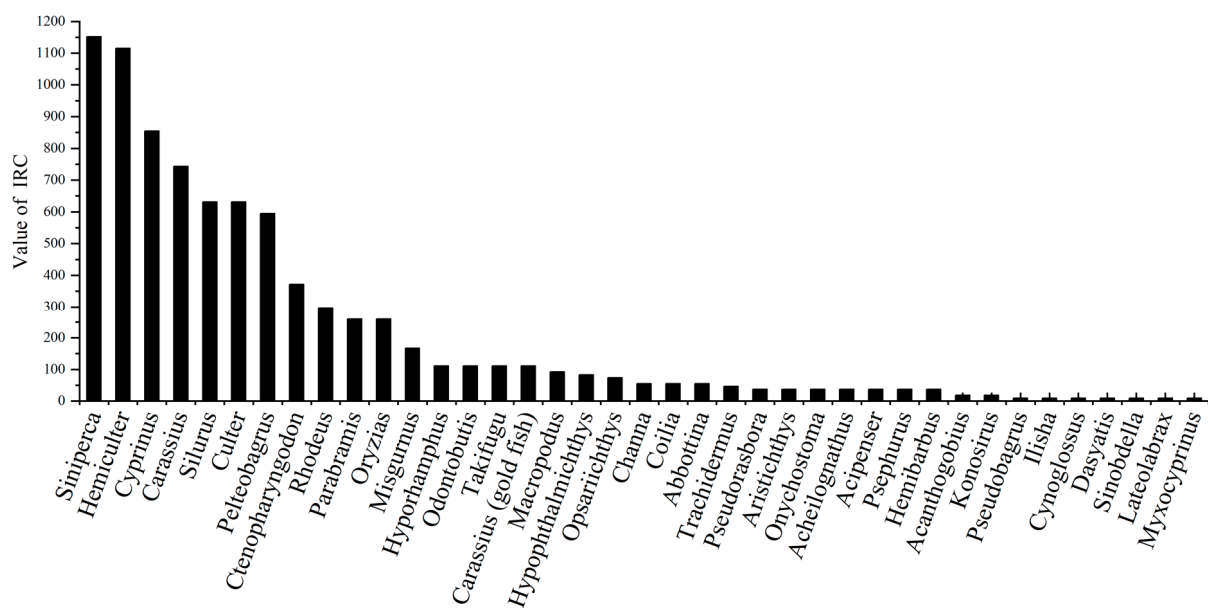


**Figure 4.** Index of Relative Commonness (IRC) values calculated for all statistical units detected in the painting dataset.

### 3.3. Pictorial Representations and Living Specimens of Major Fish Taxa

Figures 5–9 display visual records of 4 common statistical units. These include painted representations of *Siniperca* (Figure 5A), *Hemiculter* (Figure 6A,B), *Silurus* (Figure 7A,B), and *Carassius* (Figure 8A,B), alongside photographs of corresponding extant living species: *Siniperca kneri* (Figure 5B), *Hemiculter leuciscus* (Figure 6C), *Silurus asotus* (Figure 7C), and *Carassius auratus* (Figure 8C). Figure 9 compiles 9 further fish images from low-count statistical units rendered with high morphological realism. Among these examples, *Hyporhamphus* (Figure 9A), *Opsariichthys* (Figure 9B), *Sinobdella* (Figure 9C), *Rhodeus* (Figure 9D), *Macropodus* (Figure 9E), *Takifugu* (Figure 9F), and *Acheilognathus* (Figure 9G) represent small, non-dominant freshwater fishes. In contrast, *Acipenser* (Figure 9H; likely *A. sinensis* or *A. dabryanus*) and *Myxocyprinus asiaticus* (Figure 9I) are currently rare and endangered fish species.



**Figure 5.** Visual comparison of *Hemiculter*. (A) Painted depiction of *Hemiculter* from *Yu Zao Tu* by Fan Anren (Song dynasty). (B) Photographic image of a living *Hemiculter leuciscus*.

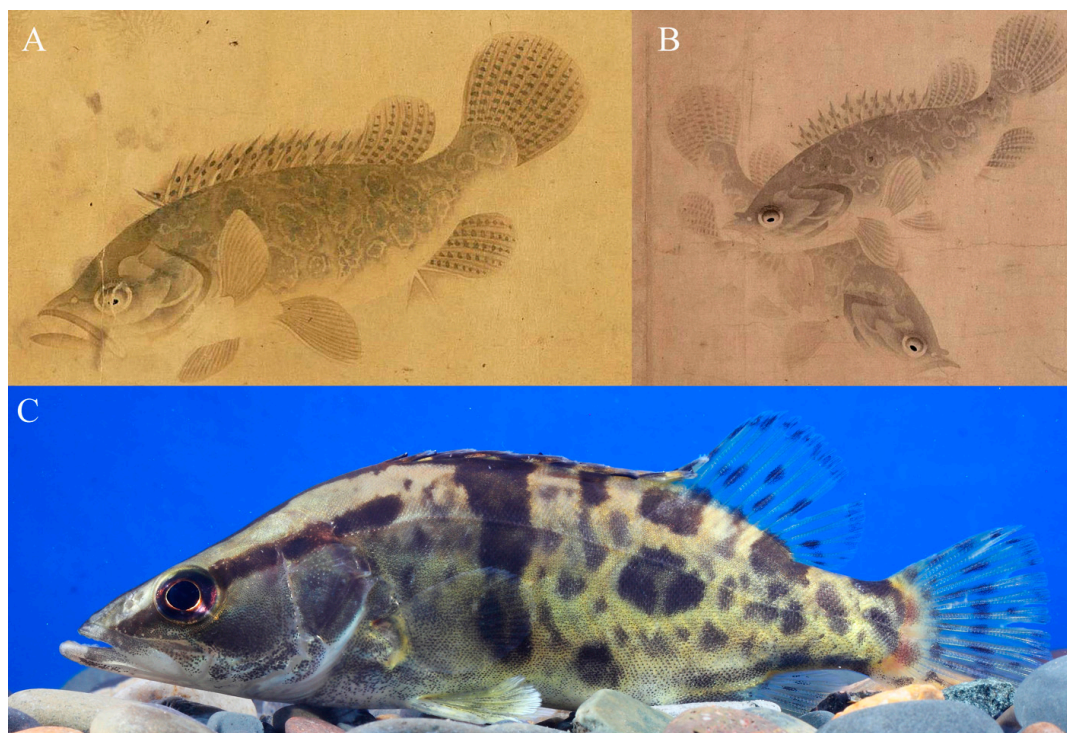


**Figure 6.** Visual comparison of *Siniperca*. (A) Painted depiction of *Siniperca* from *Qun Yu Xi Xing Tu* by Liu Cai (Song dynasty). (B) Painted depiction of *Siniperca* from *Yu Le Tu* by Zhou Dongqing (Song dynasty). (C) Photographic image of a living *Siniperca kneri*.

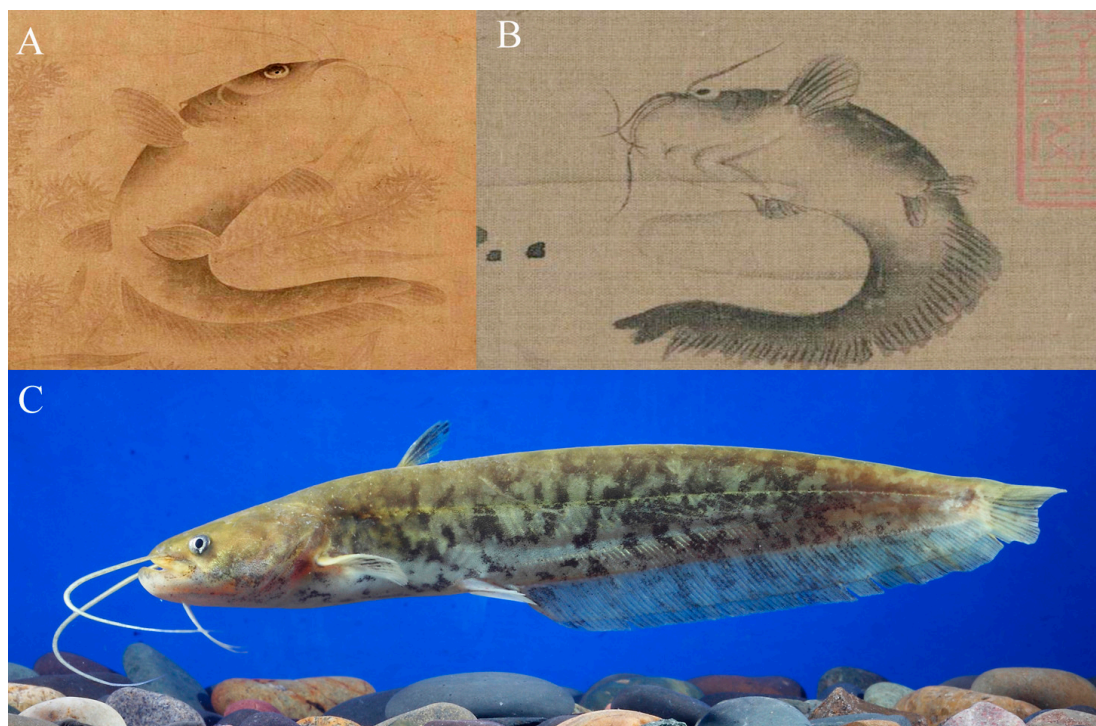


**Figure 7.** Visual comparison of *Silurus*. (A) Painted depiction of *Silurus* from *Yu Le Tu* by Zhou Dongqing (Song dynasty). (B) Painted depiction of *Silurus* from *Chun Xi Shui Zu Tu* by Chen Kejiu (Song dynasty). (C) Photographic image of a living *Silurus asotus*.

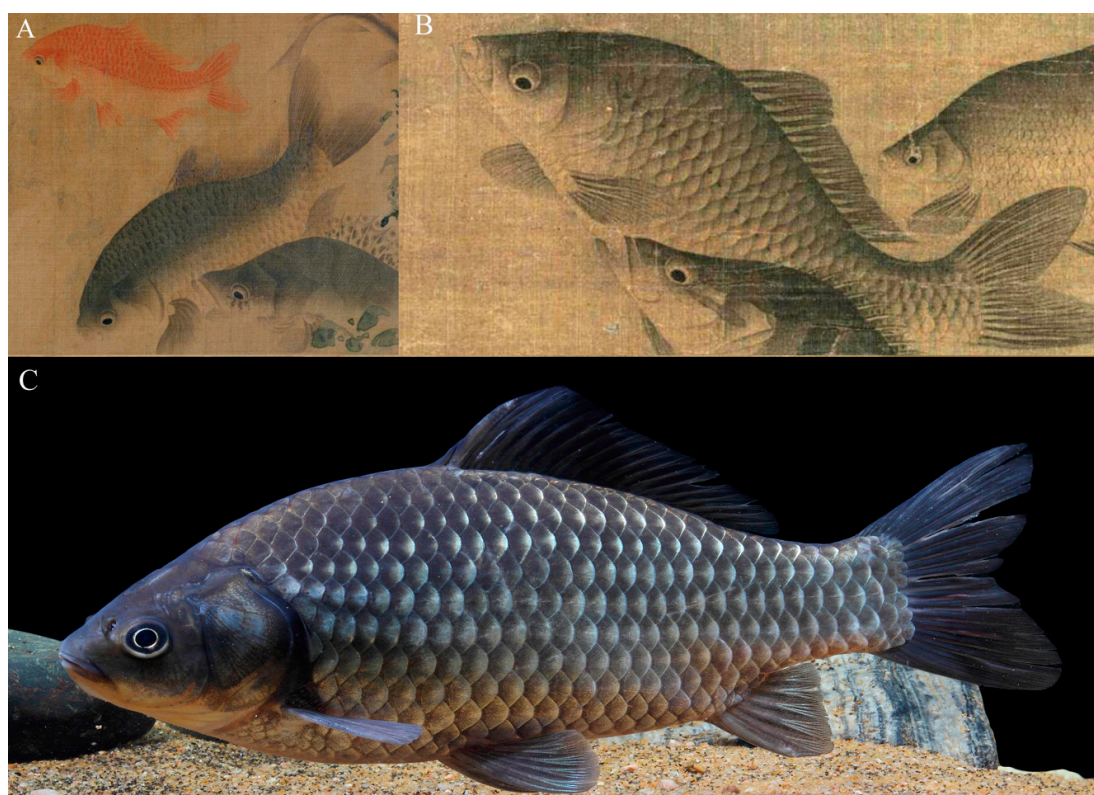


**Figure 8.** Visual comparison of *Carassius*. (A) Painted depiction of *Carassius* from *Luo Hua You Yu Tu* by Liu Cai (Song dynasty); (B) Painted depiction of *Carassius* from *Chun Xi Yu Zao Tu* (anonymous artist, Ming dynasty); (C) Photographic image of a living *Carassius auratus*.

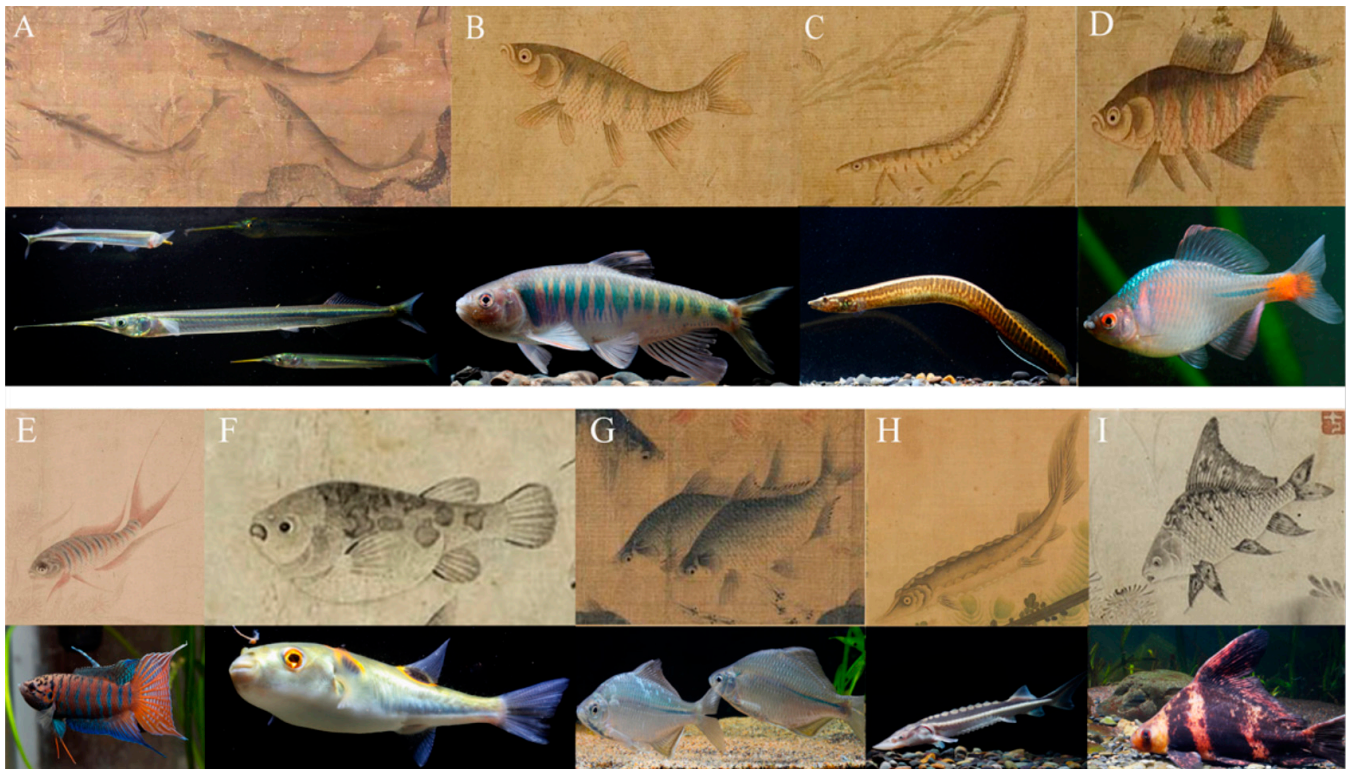


**Figure 9.** Selected low-occurrence statistical units rendered with high morphological realism in ancient paintings, paired with photographs of living conspecifics. (A) *Hyporhamphus*: painted illustration from *Zao Yu Tu* by Tang Yin (Ming dynasty) and living *Hyporhamphus intermedius*; (B) *Opsariichthys*: painted illustration from *Zao Jian You Yu Tu* by Lai An (Yuan dynasty) and living *Opsariichthys evolans*; (C) *Sinobdella*: painted illustration from *Zao Jian You Yu Tu* by Lai An (Yuan dynasty) and living *Sinobdella sinensis*; (D) *Rhodeus*: painted illustration from *Zao Jian You Yu Tu* by Lai An (Yuan dynasty) and living *Rhodeus ocellatus*; (E) *Macropodus*: painted illustration from *Yu Le Tu* by Zhou Dongqing (Song dynasty) and living *Macropodus opercularis*; (F) *Takifugu*: painted illustration from *Bai Yu Tu* (anonymous artist, Ming dynasty) and living *Takifugu ocellatus*; (G) *Acheilognathus*: painted illustration from *Luo Hua You Yu Tu* by Liu Cai (Song dynasty) and living *Acheilognathus macropterus*; (H) *Acipenser*: painted illustration from *Yu Le Tu Juan* by Katsushika Hokusai (Japanese Edo period) and living *Acipenser dabryanus*; (I) *Myxocyprinus*: painted illustration from *Luo Hua Bai Yu Tu* (anonymous artist, Ming dynasty) and living *Myxocyprinus asiaticus*.

#### 4. Discussion

Ancient paintings are vulnerable to degradation over long timescales; accordingly, fewer artworks have survived from more distant historical periods. As a result, the Qing-dynasty sample is the largest, exceeding the combined total of Song-, Yuan-, and Ming-dynasty paintings. Total fish occurrence counts were also highest for Qing-dynasty paintings, roughly equalling half of the summed counts for the three earlier dynasties. Paradoxically, Qing-era paintings contained the lowest genus-level richness among the four dynastic groups.

A broad temporal trend emerges from the Song to Qing dynasties: pictorial compositions became progressively more compact, and fewer fish taxa were represented. During the Song dynasty, the imperial painting academy established flower-and-bird painting (including swimming-fish motifs) as an independent artistic genre. Under the influence of this highly naturalistic academic style, painters closely observed fishes, birds and plants in nature and aimed to faithfully reproduce external morphological features. Song- and Yuan-dynasty artworks commonly depict fish schools within expansive landscape settings. Most Qing-dynasty swimming-fish paintings adopt small-scale compositions or close-up

views featuring only a small number of individual fish. During the Song–Yuan period, paintings contained an average of 4.04 fish statistical units, whereas Qing-dynasty paintings averaged only 1.58 statistical units. When each individual fish figure depicted within each painting was included in the statistics, Song–Yuan paintings showed a mean of 22.88 individual fish figures per artwork, compared with merely 5.67 for Qing-dynasty paintings. The Song dynasty represented the apex of academic court painting, distinguished by refined brushwork and an emphasis on naturalistic likeness. By contrast, Qing-dynasty literati painting expanded rapidly; literati artists prioritised subjective emotional expression over visual resemblance to real-world subjects [14]. Observed differences in fish occurrence patterns within paintings across dynasties may be associated with these broad-scale stylistic shifts in Chinese painting traditions.

Based on IRC outputs, statistical units were sorted into four occurrence categories within paintings: common, frequent, occasional, and rare. Among the 2 common and 14 frequent statistical units within paintings, 11 statistical units (*Siniperca*, *Hemiculter*, *Carassius*, *Cyprinus*, *Pelteobagrus*, *Ctenopharyngodon*, *Silurus*, *Culter*, *Rhodeus*, *Parabramis*, and *Oryzias*) appeared within paintings from all four investigated dynastic periods (Song, Yuan, Ming, and Qing).

*Siniperca* constitutes a highly valued food-fish group. Its Chinese common name bears phonetic similarity to the word for “honour”, so the genus enjoyed particular cultural favour in pre-modern China. As early as the Tang dynasty, the poet Zhang Zhihe praised the fine flavour of *Siniperca* in his poem *Yugezi* (“A Fisherman’s Song”). No historical documents confirm human aquaculture of *Siniperca* before the Qing dynasty; nevertheless, abundant wild populations made it a widespread food fish in ancient China. The Song-dynasty text *Dongjing Meng Hua Lu* records that *Siniperca* were already regularly served in urban restaurants during the Song era.

*Hemiculter* is broadly distributed across freshwater habitats throughout China and ranks among the most ubiquitous small wild freshwater fishes. Textual records for *Hemiculter* can be traced to the 3rd century BCE Chinese classic *Zhuangzi*. *Carassius* also achieved high occurrence counts; wild populations are dense and readily captured. By the Eastern Jin dynasty, the idiom “*Carassius auratus* crossing the river” was already used to describe objects or people occurring in overwhelming numbers. In addition, *Carassius auratus* represents the ancestral wild species from which ornamental goldfish were domesticated in China.

*Oryzias* and *Rhodeus* are also widely distributed across major Chinese river basins. *Oryzias* represented the smallest-bodied taxon identified within our dataset. Lacking substantial food value, *Oryzias* were generally not targeted by fishers. Accordingly, painters in our corpus consistently portrayed *Oryzias* from a bird’s-eye perspective (the viewpoint of an observer standing on the riverbank), rather than lateral profile views. *Rhodeus* similarly carries limited economic value, yet Song- and Yuan-dynasty painters rendered its external morphology in considerable detail. For instance, the bitterling painted by Yuan-dynasty artist Lai An in *Zao Jian You Yu Tu* displays diagnostic morphological traits precise enough to permit species-level identification as *Rhodeus ocellatus*.

*Silurus* and *Pelteobagrus* both belong to *Siluriformes*. Texts as old as the 6th-century BCE poetry compilation *Shijing* (*Classic of Poetry*) contain references to these 2 statistical units. Both produce tender flesh with few intermuscular bones and have remained popular food fishes from antiquity to the present.

*Cyprinus* (predominantly common carp, *Cyprinus carpio*) occupies a distinctive position within Chinese cultural traditions. The Chinese character for carp shares phonetic similarity with a word meaning “benefit”, making carp a cultural symbol of auspiciousness and material abundance. The folk legend of “the carp leaping over the Dragon Gate” further

linked carp imagery to career advancement and official success. Nevertheless, our analysis demonstrates that carp were infrequently depicted within Song- and Yuan-dynasty paintings and are entirely absent from Northern Song artworks. Occurrence counts increased markedly only after the Ming dynasty. This pattern may reflect lasting cultural impacts of a Tang-dynasty ban: because the pronunciation for carp (li) resembled the imperial family surname Li, the Tang state prohibited private carp cultivation and consumption [10]. This policy severely constrained carp-rearing and carp-eating customs, and its downstream cultural effects may have persisted into the Song period. Consistent with this interpretation, *Dongjing Meng Hua Lu* lists dozens of common food fish taxa sold in Northern Song urban markets but makes no mention of carp.

Beyond the taxa discussed above, several other fish groups depicted in ancient paintings deserve scholarly attention, most notably goldfish. Deliberate artificial breeding of goldfish began in China no later than the Southern Song dynasty. The Southern Song text *Mengliang lu* documents multiple colour morphs, including silvery-white variants, that already existed at that historical period. Our analysis of ancient paintings shows that the red-coloured variant *Carassius auratus* (still retaining the body shape of wild crucian carp) already appears within the Northern Song scroll *Luohua Youyu Tu Juan* (Figure 8A). Artistic depictions matching the body morphology of modern goldfish do not emerge until Qing-dynasty paintings. Goldfish portrayed in Qing-era works exhibit red, black, white and additional colour morphs, clearly distinguishable from the grey-black pigmentation of wild crucian carp. Compared with wild *Carassius auratus*, domestic goldfish display greater fin-shape diversity, elongated fins, enlarged eyes, and shorter, deeper body profiles. Prior scholarship suggests goldfish were introduced to Japan around the 16th century, during the Ming dynasty [15]. Although colour variants of *Carassius auratus* were discovered and subjected to targeted selective breeding well before the Song dynasty, modern goldfish likely did not originate prior to the Ming dynasty.

Several rare fish taxa portrayed in paintings, including *Hyporhamphus*, *Odontobutis*, *Macropodus*, *Opsariichthys*, *Hemibarbus*, *Acanthogobius*, *Konosirus*, *Ilisha*, *Dasyatis*, *Sinobdella*, and *Myxocyprinus*, were not mainstream subjects of traditional fish paintings. No historical records document their cultivation or consumption by humans, and they may have been encountered only rarely in daily life in antiquity. Nevertheless, their painted forms closely match the morphological traits of the actual organisms. How painters obtained such accurate visual information remains unclear.

Katsushika Hokusai's scroll *Yule Tu Juan* meticulously illustrates the dorsal morphology of *Psephurus gladius*. No surviving historical records indicate that Hokusai ever travelled to China, so his illustration of *Psephurus gladius* was likely copied from earlier Chinese paintings. Two pre-existing artworks are known to depict *Psephurus gladius*: the Song-dynasty scroll *Sou Shan Tu*, and the 18th-century Japanese volume *Maoshi Pinwu Tu Kao*. The Japanese rendering is highly schematic and carries limited documentary value, whereas *Sou Shan Tu* only portrays the species' ventral surface. A possibility is that rendered Chinese paintings showing the dorsal anatomy of *Psephurus gladius* existed prior to Hokusai's lifetime but were subsequently lost. An alternative possibility is that morphological knowledge of these fishes could have circulated cross-culturally via textual descriptions rather than through copied paintings.

All ancient paintings analysed in this study belong to the conventional "swimming fish" motif category, rather than zhiguai (fantastic creature motifs) or mythological themes. Painters appear to have selected subject fish via two major pathways. The first pathway involved copying earlier artworks and generating derivative new compositions built upon these prior models. The second pathway involved depicting fish taxa that painters regularly encountered within everyday life. The Song-dynasty text *Dongjing Meng Hua Lu* supports

high-count taxa within ancient paintings, such as *Siniperca*, *Carassius*, and *Silurus*, which already appeared frequently within Northern Song marketplaces and on ordinary dining tables. These fishes were more likely to be captured by fishers, brought to urban markets, and encountered by painters.

In summary, genus-level occurrence patterns within ancient paintings primarily reflect cultural recognition and familiarity among past human societies toward different fish taxa. These artistic patterns do not serve as a direct mirror of actual riverine fish community assemblages during historical periods. On the other hand, a qualitative comparison between genus-level occurrence patterns extracted from paintings and modern fishery survey datasets for the Haihe [16–19], Yellow [20–23], Huaihe [24–26], Yangtze [27], Qiantang [28–30], Pearl [31,32], and Minjiang [33] river basins reveals that some taxa frequently depicted in ancient paintings, such as *Hemiculter*, *Carassius*, and *Cyprinus*, are also widely documented across major Chinese river drainage basins. How fish distributions derived from paintings should be calibrated against empirical survey data—so that ancient paintings can be applied more rigorously to modern biogeographical research—represents an ongoing research direction in this field.

## 5. Conclusions

Through genus-level taxonomic identification and quantitative IRC analysis of 101 fish-themed Chinese paintings spanning the Song–Qing dynasties, this study characterises taxonomic composition and temporal dynamics of fish imagery preserved within ancient Chinese paintings. We identified a total of 39 statistical units (including 38 genera and goldfish) belonging to 23 families and nine orders. Across all four dynastic periods, Cypriniformes, Perciformes, and Siluriformes were the dominant groups represented in paintings. *Siniperca* and *Hemiculter* constituted the two most common statistical units within paintings overall. Eleven statistical units appear continuously within paintings from the Song to Qing dynasties. Distinct dynastic-period patterns in fish depiction are evident. Song- and Yuan-dynasty paintings capture more fish genera. By contrast, Qing-dynasty paintings represent fewer fish genera. Consequently, even though the Qing-dynasty painting sample is the largest and yields the highest total fish occurrence counts, it exhibits the lowest genus-level taxonomic diversity. Taxa frequently portrayed in ancient paintings mostly correspond to commonly consumed fish species. On the other hand, several less-conspicuous fish genera, for which no historical records of cultivation or consumption survive, are rendered with striking accuracy. In summary, complementing written textual archives, ancient paintings serve as a valuable complementary resource for investigating pre-modern human observational understanding of nature and the cultural importance of different fish taxa across successive historical periods.

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