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# Species diversity and distribution of genus *Pampus* (Pelagiaria: Stromateidae) based on global mitochondrial data

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Due to the highly similar external morphology of the *Pampus* species, misidentifications frequently occur and hinder the understanding of the taxonomy and species distributions of the genus. In this study, we generated 271 mitochondrial sequences and obtained 1,226 sequences from the public databases to understand the species diversity and distributions of the genus *Pampus*. Most phylogenetic analyses and species delimitations congruently concluded seven valid species within the genus *Pampus* (i.e., *P. argenteus*, *P. candidus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus*). Sequences of *P. argenteus* are reported through the northern South China Sea to the Japan Archipelago, which covered the type locality of *P. echinogaster*. Sequences of *P. echinogaster* in the public databases are all identified as *P. argenteus*, suggesting that the species should be synonymized with *P. argenteus*. Furthermore, sequences of *P. griseus* were identical to our *P. cinereus* data and, therefore, should be treated as a synonym of the latter. Inference on divergence time and ancestral distribution implied that the genus *Pampus* originated in the central Indo-Pacific region around 8.35–11.33 million years ago (the late Miocene), associated with the rise of the Indonesian–Australian Archipelago biodiversity hotspot. The divergence between *P. cinereus* and *P. liuorum* dated back to 1.20–1.72 million years ago, which might be related to glacial isolation during the Mid-Pleistocene transition.

KEYWORDS

**mitochondrial data, *Pampus*, species distribution, taxonomy, the Indonesian-Australian Archipelago, the middle Miocene transition**

# Introduction

The genus *Pampus* Bonaparte, 1834, of the family Stromateidae Rafinesque, 1810, is distinct in having a compressed, silvery body, elongated pelvic bone, absence of pelvic fins, and more than five blade-like spines before their falcate dorsal and anal fins [but spine is absent in *Pampus chinensis* (Euphrasen, 1788), Liu et al., 2002; Liu et al., 2013a]. Members of the genus *Pampus* are commercially important fishes in the Indo-West Pacific area (Liu et al., 2002; Radhakrishnan et al., 2019; Roul et al., 2021). There have been concerted efforts to study their reproductive biology, evolution, and population genetics of the *Pampus* species (e.g., Dadzie et al., 2000; Gupta, 2020; Fan et al., 2022). Nevertheless, the chaotic taxonomies and misidentifications have hindered our understanding of the biology and evolution of this genus (Liu et al., 2013a; Radhakrishnan et al., 2019; Wei et al., 2021).

Due to the highly similar external morphology of the *Pampus* species, misidentifications frequently occur and greatly affect the understanding of the taxonomy and species distributions of the genus (Wei et al., 2021). Haedrich (1967) recognized three species in the genus *Pampus*, i.e., *Pampus argenteus* (Euphrasen, 1788), *Pampus echinogaster* (Basilewsky, 1855), and *P. chinensis*, and assigned many species names as synonyms of the three species. With recent efforts, *Pampus cinereus* (Bloch, 1795), *Pampus candidus* (Cuvier, 1829), and *Pampus punctatissimus* (Temminck & Schlegel, 1845) are resurrected as valid species; *Pampus liuorum* Liu & Li, 2013, and *Pampus minor* Liu and Li, 1998, are published as new species (Liu and Li, 1998a; Liu and Li, 1998b; Liu et al., 2013a; Liu et al., 2013b; Liu and Li, 2013), demonstrating that the genus *Pampus* is actually a more diverse group. Our previous study, Wei et al. (2021), confirmed the validities of seven species in the genus *Pampus*, viz., *P. argenteus*, *P. candidus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus*. However, validities of several species names, e.g., *P. echinogaster* and *Pampus nozawae* (Ishikawa, 1904), and *Pampus griseus* (Cuvier, 1833), remained unclear. Haedrich (1967) considered *P. echinogaster* as a species only found in China, Korea, and Japan, which is distinct from *P. argenteus* widely distributed in the Indo-West Pacific. The idea is widely used by taxonomic works, and for decades, the two species have been treated as different valid species (e.g., Lindberg and Krasyukova, 1989; Liu et al., 2002; Nakabo, 2002). Although morphological comparison indicated that *P. echinogaster* is nearly identical to the *P. argenteus* neotype except in a few metrical characters, the two species are still treated as different valid species by Liu et al. (2013a) because of the proposed north–south difference in their distributions: *P. argenteus* was considered distributed in offshore Guangdong and probably from Southeast Asia (Liu et al., 2013a); *P. echinogaster* was considered never found southward to the Taiwan Strait (Nakabo, 2002). Li et al. (2017) also proposed *P. echinogaster* as a valid species in the Northwest Pacific, but the fin ray, gill raker, and vertebral counts of their specimens overlap with the neotype of *P. argenteus* designated by Liu et al. (2013a). *P. nozawae* is published based on a lost type specimen from Hokkaido, northern Japan. The name has been used by several taxonomic works and is recently validated by Jawad and Liu (2017) based on a comparison of the axial skeleton. Although Jawad and Liu (2017) stated several differences between *P. nozawae* and its congeners, the examined specimens are collected from Southeast Asia instead of Japan, which presumed *P. nozawae* as a species broadly distributed through Southeast Asia to Japan. Roul et al. (2021) resurrected *P. griseus* (Cuvier 1833) and assumed that *P. griseus* inhabits the Indian Ocean, whereas its close relative, *P. cinereus*, only inhabits the western Pacific, although it is incongruent with the statement by Bloch and Schneider (1801) that *P. cinereus* inhabits waters around Tranquebar (i.e., Tharangambadi, India). Obviously, taxonomic issues of these *Pampus* species are accompanied by potential confusion on species distributions. A thorough review of global species diversity and distribution of the genus *Pampus* is necessary.

Molecular tools have been utilized to distinguish the *Pampus* species and studied their phylogeny and population genetics (e.g., Sun et al., 2012; Li et al., 2019; Roul et al., 2021). Over 1,500 DNA sequences of the genus *Pampus* have been deposited on GenBank and the Barcoding of Life Database (BOLD) with well-documented sampling localities in the databases and published studies, which provided a suitable dataset for studying species diversity and distribution of the genus *Pampus*. However, misidentification of the *Pampus* sequences frequently occurs (Roul et al., 2021; Wei et al., 2021), which greatly impedes the progress to clarify their taxonomy and distributions. In our previous study, Wei et al. (2021) provided reliable barcodes of cytochrome oxidase unit I (*COXI*) and cytochrome *b* (*Cytb*) from 74 specimens of seven *Pampus* species (i.e., *P. argenteus*, *P. candidus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus*). The specimens have been properly identified morphologically based on taxonomic works of the genus (i.e., Liu and Li, 1998a; Liu et al., 2013b; Liu et al., 2013a; Liu et al., 2013b; Radhakrishnan et al., 2019). A comparison of these barcodes with the global sequence data could provide valuable insight into the species diversity and distribution of the genus *Pampus*. We performed genetic comparisons on the mitochondrial sequences of the *Pampus* species from this study, Wei et al. (2021), GenBank, and BOLD to clarify the global species diversity and distribution of the genus *Pampus*. Inference on divergence times and ancestral distribution were also performed to provide a new perspective on the origin of the *Pampus* species.

# Materials and methods

## Species diversity and distributions

A workflow for clarifying species diversity and distributions of the genus *Pampus* is illustrated in Figure 1. In brief, we used

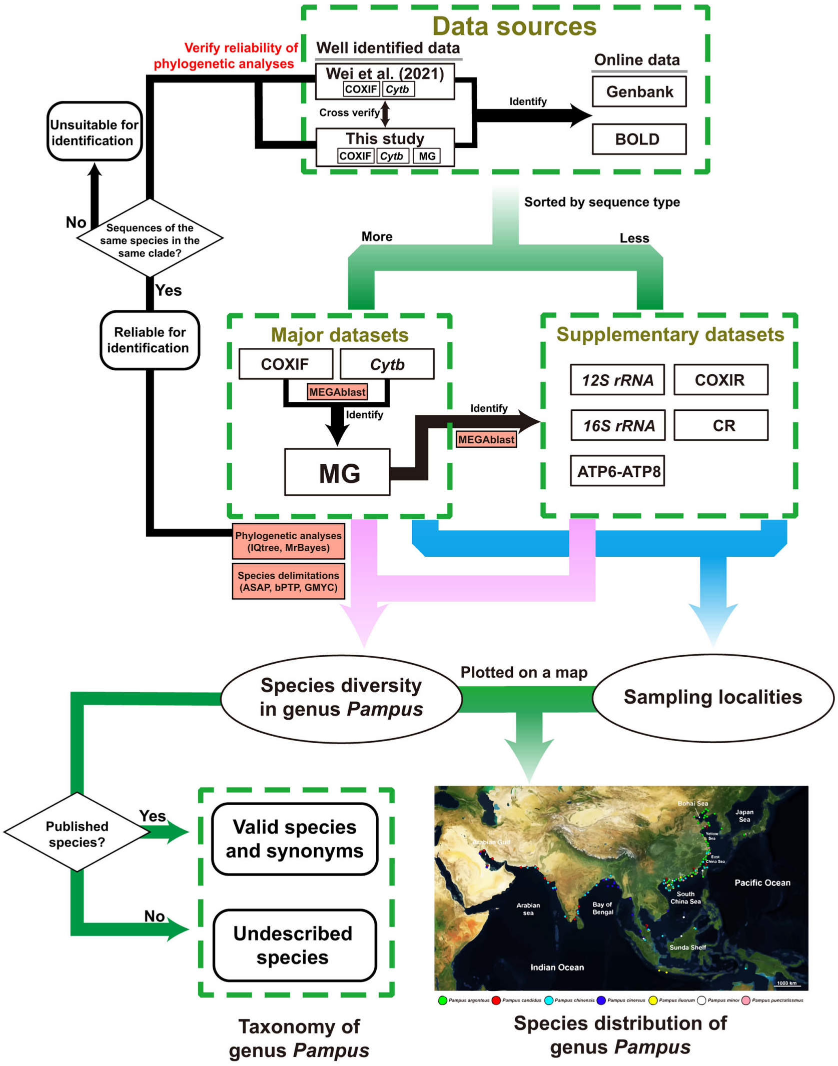

FIGURE 1
A workflow for exploring the species diversity and distributions of genus *Pampus* using the global mitochondrial data.

the properly identified sequences from this study and Wei et al. (2021) to identify the public sequence data and explore the global species diversity of the genus *Pampus*. Sampling localities of the sequences identified to species level were plotted on a map to illustrate the distributions of the *Pampus* species.

## Acquisition of local data

From 2009 to 2021, a muscle sample inventory of the *Pampus* species containing 209 muscle tissue samples from China, Malaysia, India, Iraq, Kuwait, and Bahrain was established in the Institute of Oceanology, Chinese Academy of Sciences (IOCAS). Most of the samples have either voucher specimens deposited in IOCAS or specimen photos taken upon collection (e.g., Figure 2). Among the 209 samples, 74 had been used in our previous study (Wei et al., 2021). *COXI* and *Cytb* sequences of the other 135 samples were obtained in this study using Sanger sequencing. Total genomic DNA was extracted from the muscle samples using TaKaRa MiniBEST Universal Genomic DNA Extraction Kit (TaKaRa Inc., Mountain View, CA, USA) following the product manual. Polymerase chain reactions (PCRs) and Sanger sequencing were performed by Tsingke Ltd. (Qingdao, China). In addition to the 135 samples, mitogenome (MG) sequences were also obtained from muscle tissues of five additional specimens of *P. argenteus* (specimen numbers: 20120541 and 20181206004), *P. liuorum* (specimen numbers: 20120541 and 20181206004), and *P. punctatissimus* (specimen number: 20181206007). The total genomic DNA of the muscle tissues was also extracted using TaKaRa MiniBEST Universal Genomic DNA Extraction Kit. The extractions were sent to SCGene Ltd. (Guangzhou, China) for next-generation

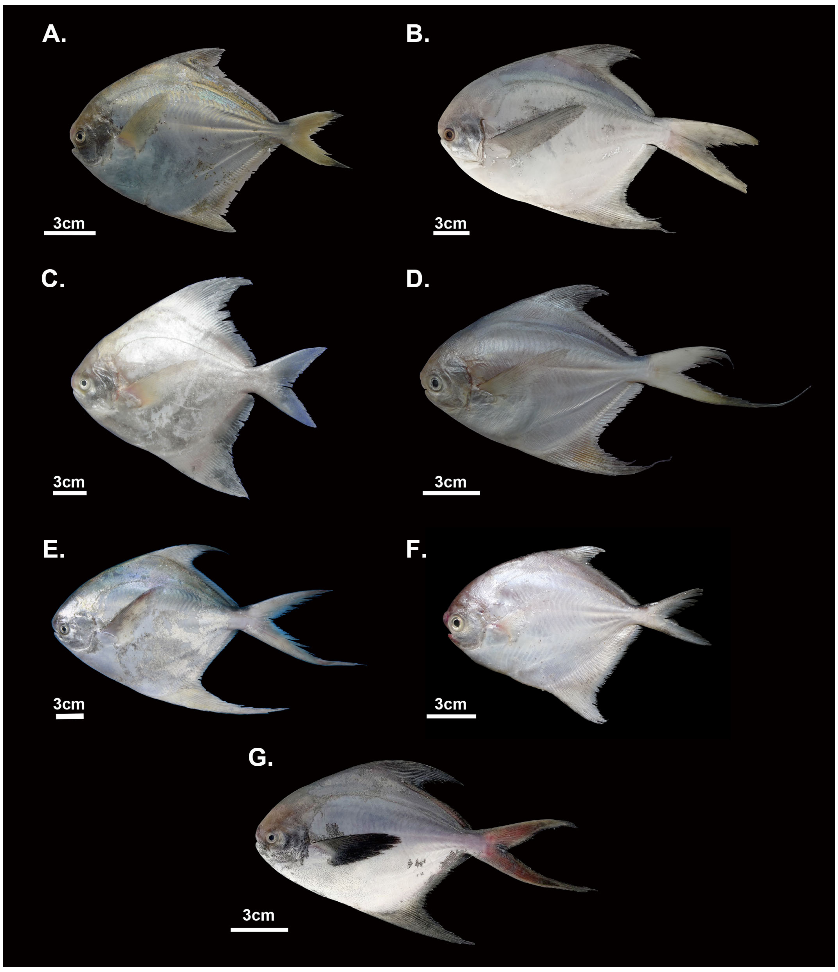

FIGURE 2
Photographs of the seven valid *Pampus* species. **(A)** *Pampus argenteus* (20120469). **(B)** *Pampus candidus* (IOCASF000292). **(C)** *Pampus chinensis* (201006001). **(D)** *Pampus cinereus* (20120481). **(E)** *Pampus liuorum* (HBRF03-036). **(F)** *Pampus minor* (20120502). **(G)** *Pampus punctatissimus* (IOCASF000289).

sequencing. All the details regarding DNA extraction, primers, polymerase chain reaction, sequencing methods, and assembly of the *COXI*, *Cytb*, and mitogenomes are given in Appendix S1. All the samples were identified by J. Liu and J. Wei based on our previous taxonomic works (Liu and Li, 1998a; Liu and Li, 1998b; Liu et al., 2013a; Liu et al., 2013b; Liu and Li, 2013). The obtained sequences were compared with Wei et al. (2021) to ascertain correct identification. The well-identified local data was used as the main reference data to identify the online mitochondrial data of the *Pampus* species.

## Acquisition of public data

Mitochondrial sequences from GenBank and BOLD were collected by searching with the keyword "*Pampus*" in combination with the names of mitochondrial markers, e.g., "cytochrome *c* oxidase subunit I", "cytochrome *b*", "control region", and "mitochondrion". Sequences of the other stromateids (i.e., genera *Stromateus* Linnaeus, 1758 and *Peprilus* Cuvier, 1829) were also collected from GenBank as outgroups for molecular analyses.

## Data sorting, filtering, and alignment

All the sequences were sorted into datasets by sequence types in Geneious Prime® v2022.1.1 (Biomatters Ltd., Auckland, New Zealand). Because the *COXI* dataset contained sequences located in different gene regions, we split the *COXI* dataset by their regions, namely, the *COXIF* (the forward region of *COXI*) and *COXIR* (the rear region of *COXI*) datasets. Due to extensive unaligned regions and insertions in non-coding genes [e.g., 12S ribosomal RNA (*12S rRNA*) and 16S ribosomal RNA (*16S rRNA*)] and control region (CR) of the mitogenomes, we only used their protein-coding genes to form the MG dataset for molecular analyses, i.e., ATP synthase membrane subunit 6 (*ATP6*), ATP synthase membrane subunit 8 (*ATP8*), *COXI*, cytochrome *c* oxidase subunit II (*COXII*), cytochrome *c* oxidase subunit III (*COXIII*), *Cytb*, and NADH-ubiquinone oxidoreductase chain 1–6 and 4L (*ND1–6* and *ND4L*). The protein-coding gene sequences of each mitogenome were extracted in the Geneious Prime and concatenated in the SequenceMatrix v1.7.8 (Vaidya et al., 2011). Information on the datasets is summarized in Table 1 and detailed with accession number, sampling localities, and corresponding references in Appendix S2. The major datasets (i.e., the *COXIF*, *Cytb*, and MG datasets) contained more sequences, and sampling localities were used for the molecular analyses and studying the distributions of the *Pampus* species, while the supplementary datasets with unique sampling localities were retained for studying species distributions (Table 1). Sampling localities corresponding to the sequences were plotted on a map to illustrate the distributions of the *Pampus* species (Figure 3).

Alignments of the datasets were performed using the MAFFT v7.388 (Katoh and Stanley, 2013) plugin in Geneious Prime with default settings; external gaps were treated as missing data. Any protein-coding gene sequences with reading frameshift, extensive regions of indels, or unaligned nucleotides were excluded from the datasets. The datasets were then compared with GenBank sequences using the MegaBLAST (Morgulis et al., 2008) plugin in Geneious Prime® (Biomatters Ltd.); the first 20 hits with over 98% identical sites were used for preliminary identification. Sequences of non-stromateid species were excluded from the datasets.

## Species identification, phylogenetic analyses, and species delimitations

Species identifications were mainly performed using the MegaBLAST plugin to compare the sequences with a local database set up in Geneious Prime. The first 20 hits with over 98% identical sites were used for identification. The local database was mainly formed by the well-identified *COXIF*, *Cytb*, and mitogenome sequences from this study and Wei et al. (2021). The mitogenomes from public data were also added to the local database after proper identification. Due to the lack of corresponding reference sequences from this study and Wei et al. (2021), sequences of the supplementary datasets were identified based on the mitogenomic data of the local database. Wei et al. (2021) indicated that *COXIF* sequences of *P. cinereus* and *P. liuorum* have very few differences, which might affect the ability of MegaBLAST to identify the two species. Therefore, *COXIF* sequences of the two species were identified based on the maximum likelihood (ML) tree.

Phylogenetic analyses and species delimitations were performed on the major datasets (Table 1). Whenever possible, ML trees of the supplementary datasets were also generated to eliminate potential misidentification by MegaBLAST. The ML trees are given in Appendix S3. Sequence variation indices of the major datasets (i.e., number of polymorphic sites, parsimony informative sites, and indels) were calculated using DnaSP v6 (Rozas et al., 2017). In the subsequently mentioned analyses, each gene of the MG dataset was treated as a partition. Substitution saturation of the datasets was examined on the three-codon position using the method in DAMBE v7.2.25 of Xia et al. (2003) (Xia, 2018). Best-fit substitution models were selected using jModelTest v2.1.10 (Darriba et al., 2012) based on the Bayesian information criterion (Schwarz, 1978). The results of saturation and model tests are given in Appendix S4. ML trees were inferred in IQtrees v1.6.12 (Nguyen et al., 2015), with 1,000 bootstrap (BS) replicates to estimate the BS values of nodes. For Bayesian inference (BI) trees, two independent Markov chain Monte Carlo (MCMC) runs were performed in MrBayes v3.2 (Ronquist et al., 2012), with four chains for 500,000 generations, sampling every 100 generations. The maximum clade credibility tree of the two runs was generated in MrBayes with the first 25% of samples discarded as burn-in.

TABLE 1 Information from the eight datasets collated from 1,497 mitochondrial sequences of genus *Pampus* used in this study.

| **Datasets** | | **Number of *Pampus* sequences** | **Number of sampling localities** | **Number of *Pampus* species** | **Sequence length (bp)** |
|---|---|---|---|---|---|
| Major datasets | *COXIF* | 499 | 98 | 7 | 440–684 |
| | *Cytb* | 447 | 52 | 7 | 401–1,137 |
| | MG | 27 | 6 | 7 | 16,534–18,062 |
| Supplementary datasets | *12S rRNA* | 9 | 2 | 4–5# | 169–441 |
| | *16S rRNA* | 86 | 11 | 5–6# | 391–564 |
| | *ATP6-ATP8* | 31 | 7 | 2 | 838–842 |
| | *COXIR* | 105 | 13 | 7 | 472–643 |
| | CR | 293 | 33 | 7 | 358–978 |
| Total | | 1,497 | 126 | 7 | 169–18,062 |

#Identities of some sequences of this dataset are uncertain, being either *P. cinereus* or *P. liuorum*.

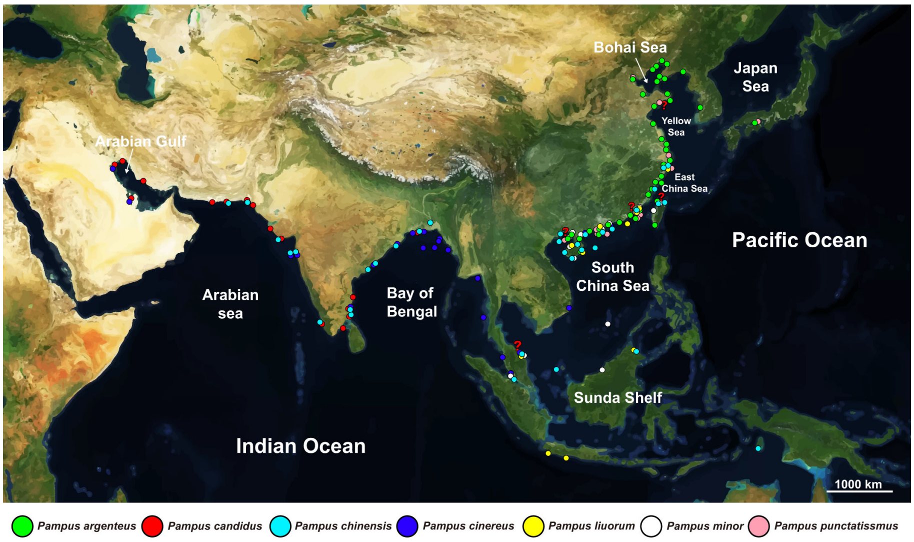

FIGURE 3
Distributions of the *Pampus* species based on sampling localities of the eight mitochondrial datasets used in this study. The basic map is generated in Mapbox (https://www.mapbox.com/). Spots on map denote sampling localities of the seven valid species. Geographically close localities are merged into one spot. Red question marks denote that *Pampus candidus* might not distribute in these sampling localities.

Species delimitations were performed using the Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021), single threshold Bayesian Poisson tree processes (bPTP; Zhang et al., 2013), and generalized mixed Yule coalescent (GMYC; Pons et al., 2006; Fontaneto et al., 2007; Fujisawa and Barraclough, 2013) methods in the itaxoTools package v6.2.1 (Vences et al., 2021). All the analyses were performed with the default setting in itaxoTools following the instruction manual (Vences et al., 2021), except that genetic distances were calculated with Kimura's two-parameter model (Kimura, 1980) instead of the default Jukes–Cantor model distance (Jukes and Cantor, 1967) in the ASAP. Notably, the ASAP of the MG dataset was deployed to each gene partition of the MG dataset, while the bPTP and GMYC were performed using trees generated with the whole MG dataset. The ML trees of the major datasets (Table 1) were used as phylogram input for the bPTP. Ultrametric trees for the GMYC of the major datasets were generated in BEAST v1.10.4 (Drummond and Rambaut, 2007). Two MCMC runs for 10,000,000 generations of each dataset were conducted with the best-fit substitution model and sampling every 1,000 generations. The constant population size model was applied following the instruction of the GMYC (Fujisawa and Barraclough, 2013). Sufficient convergences and burn-in of the runs were checked in Tracer v1.7 (http://tree.bio.ed.ac.uk/software/tracer), ascertaining that the effective sampling sizes of all the parameters were greater than 200. A maximum clade credibility tree (i.e., ultrametric tree) was generated using TreeAnnotator v1.10.4, discarding the first 10% sample as burn-in.

## Inference of divergence time

A recent phylogenetic study recovered the sister relationship of the genera *Pampus* and *Stromateus* (Arcila et al., 2021). The two genera distribute on either side of the Arabian Peninsula, where the ancient Tethys Seaway was situated. The only fossil genus of the Stromateidae, *Pinichthys* Bannikov, 1985, was also discovered around the Tethys Seaway (i.e., the Paratethys, Bannikov, 1985). These studies indicate that the stromateids might have a Tethyan origin, and the closure of the Tethys Seaway might have resulted in the isolation and divergence of *Stromateus* and *Pampus*. Therefore, we used the closure time of the Tethys Seaway [14.00 million years ago (Mya), Hamon et al., 2013] as the lower limit and the age of the oldest *Pinichthys* fossil (i.e., *Pinichthys pulcher* Bannikov, 1988, 32.00–33.70 Mya, the age of its sampling layer, Bannikov, 1988; Popov et al., 2019) as the upper limits to calibrate the time to most recent common ancestor (tMRCA) of *Stromateus* and *Pampus*. Due to the lack of mitogenome of the *Stromateus* species, we estimated the calibrated *COXI* substitution rate using an additional *COXI* dataset (the *COXIA* dataset, Appendix S3) including representative sequences of the *Stromateus* and *Pampus* species. The calibrated *COXI* rate was used for divergence inference. For substitution rate calibration, the random local clock and birth-death process model was selected as the best-fit clock and tree models based on the comparison of Bayes factors, estimated by the path sampling method in BEAST (Baele et al., 2012, Appendix S5). The fossil calibration was applied to the tMRCA of *Stromateus* and *Pampus* with an exponential distribution [mean = 5.34, offset = 14.00, 95% highest posterior density interval (HPD95): 14.14–33.7 Mya]. Two independent MCMC runs were conducted with 10,000,000 generations in BEAST v1.10.4 (Drummond and Rambaut, 2007), sampling every 1,000 generations. Sufficient convergence and burn-in of runs were checked with Tracer v1.7 and effective sampling size (ESS) values (above 200). The log file of the two runs was combined in LogCombiner v1.10.4 of the BEAST package, discarding the first 10% of samples as burn-in. The probability density of the calibrated *COXI* substitution rate was estimated from the combined log file using Tracer v1.7.

To save computational time, a representative MG sequence of each identified *Pampus* species and the outgroup *Peprilus triacanthus* (Peck, 1804) was selected to form the reduced MG dataset for divergence time inference. Following substitution rate calibration, the random local clock and the birth-death process model were also applied. The calibrated *COXI* substitution rate was applied using a normal distribution (mean = 0.0019, standard deviation = 0.0028), covering HPD95 of the rate. Substitution rates of other genes were estimated in BEAST through the MCMC runs. The ML tree of the reduced MG dataset was used as the input tree for BEAST, and the topology was fixed through the MCMC runs. Two independent MCMC runs were conducted with 100,000,000 generations, sampling every 1,000 generations. Sufficient convergence and burn-in of runs were checked with Tracer v1.7 and ESS (above 200). The tree files of the two runs were combined in the LogCombiner v1.10.4 in the BEAST package. The maximum clade credibility tree was generated in TreeAnnotator v1.10.4 of the BEAST package with the first 10% of samples discarded as burn-in.

## Ancestral distribution reconstruction

The ancestral distribution of the genus *Pampus* was inferred in RASP v4.2 (Yu et al., 2015). The ultrametric-tree file retrieved in divergence time inference was used as the input for RASP after the removal of the outgroup. The consensus tree was generated in RASP. The Indo-Pacific region was divided into three areas with different species diversities: the Indian Ocean (IO; i.e., the Arabian Sea, the Bay of Bengal, and adjacent waters), the central Indo-Pacific [CIP; i.e., the East China Sea, South China Sea, Sunda Shelf, and adjacent waters], and the Northeast Asian waters (NAW; i.e., the Japan Archipelago, Yellow Sea, Bohai Sea, and the adjacent waters). The best-fit model for ancestral reconstruction was determined using BioGeoBEARS (Matzke, 2014) in RASP, and the Statistical Dispersal-Extinction-Cladogenesis model was selected (Beaulieu et al., 2013). Therefore, the ancestral distribution was inferred using the Statistical Dispersal-Extinction-Cladogenesis model allowing six candidate states on nodes: IO, CIP, NAW, IO + CIP, CIP + NAW, and IO + CIP + NAW.

# Results

## The datasets used in this study

A total of 1,497 mitochondrial sequences of the *Pampus* species, comprised of 271 newly obtained, 1,120 published, and 106 unpublished sequences from GenBank and BOLD were collected. The *COXIF*, *Cytb*, and MG sequences newly obtained in this study were deposited in GenBank (accession numbers: *COXIF*, OP035984–OP036119; *Cytb*, OP066061–OP066192; MG, OP096421–OP096425). All the sequences were sorted into eight datasets by genes, i.e., *12S rRNA*, *16S rRNA*, *ATP6-ATP8*, *COXIF*, *COXIR*, CR, *Cytb*, and MG datasets (Table 1; Appendix S2). The *COXIF* dataset contained 499 sequences of the *Pampus* species and a single sequence of *Peprilus medius* (Peter, 1869), and their sequence length ranged from 440 to 646 bp. The dataset was aligned into a 690-bp alignment with 143 polymorphic sites, 105 parsimony informative sites, and 10.13% missing data (i.e., external gaps). The *Cytb* dataset encompassed 447 sequences of the *Pampus* species and a single sequence of *P. medius* (outgroup) (401–1137 bp), with 130 polymorphic sites, 102 parsimony informative sites, and 9.70% missing data in its 1,152-bp alignment. The 11,424-bp MG dataset included 28 mitogenomes of the *Pampus* species and an outgroup *P. triacanthus* and consisted of 13 protein-coding genes: *ATP6* (683 bp), *ATP8* (168 bp), *COXI* (1,551 bp), *COXII* (691 bp), *COXIII* (785 bp), *Cytb* (1,137 bp), *ND1* (975 bp), *ND2* (1,046 bp), *ND3* (349 bp), *ND4* (1,381 bp), *ND4L* (297 bp), *ND5* (1,839 bp), and *ND6* (522 bp), which summed up to 4,293 polymorphic sites and 3,569 parsimony informative sites. The MG dataset was reduced into having eight MG sequences for divergence time inference, i.e., the outgroup *P. triacanthus* and seven *Pampus* species identified in the major datasets (see the results below). No saturated codon position was identified in the three datasets.

## Species identification, phylogeny, and species delimitation

All sequences can be identified as the seven *Pampus* species using MegaBLAST, viz., *P. argenteus*, *P. candidus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus*, except that some *12S rRNA* and *16S rRNA* sequences were uncertainly identified as either *P. cinereus* or *P. liuorum* due to their short sequence lengths and the low numbers of mutations of the two genes. All the ML trees reconstructed from the major datasets (i.e., the *COXIF*, *Cytb*, and MG datasets, Figure 4) identified seven clades in the genus *Pampus*. All the sequences of this study and Wei et al. (2021) were assigned to correct clades corresponding to their morphological identities in the ML trees, which suggests the capabilities of these trees to identify the *Pampus* species (Figure 4;

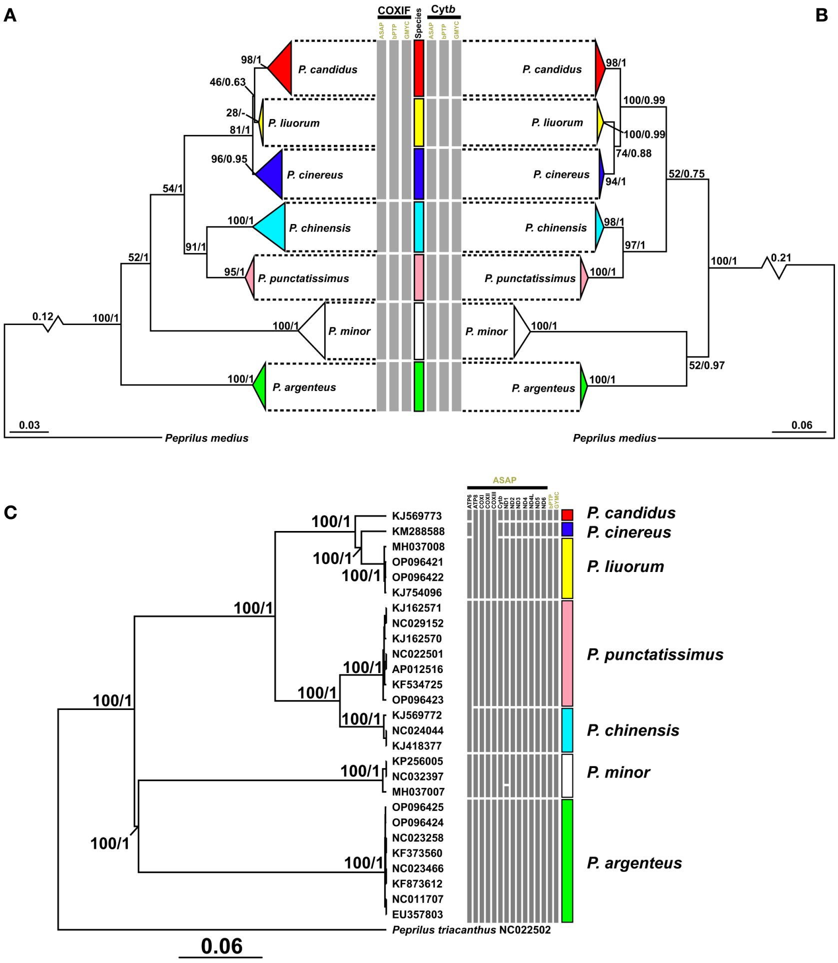

FIGURE 4
ML trees of the *COXIF* **(A)**, *Cytb* **(B)**, and MG **(C)** datasets. Bootstrap values and posterior probabilities obtained in ML and BI analyses are shown on each node. The broken lines indicate that these branches are condensed, and the original branch lengths are shown on these branches. ML, maximum likelihood; BI, Bayesian inference.

Appendix S3). The correct identities of all the analyzed sequences are summarized in Appendix S2. *Cytb* sequences of *P. argenteus sensu* Sun et al. (2012) encompassed three species, i.e., *P. liuorum* from China, *P. cinereus* from Myanmar and Thailand, and *P. candidus* from India and Pakistan. All the sequences of *P. echinogaster* were identified as *P. argenteus* (Appendix S2). *COXIF* sequences of *P. echinogaster sensu* Li et al. (2017) were nested within the *P. argenteus* clade (Appendix S2), while those of *P. argenteus sensu* Li et al. (2013) were nested within the *P. candidus* clade (Appendix S2). Both *COXIF* and *Cytb* sequences of *P. griseus* from Roul et al. (2021) were identified as *P. cinereus*, while *P. cinereus sensu* Roul et al. (2021) were *P. liuorum* (Appendix S2). Sequences annotated as *P. nozawae* were identified as either *P. liuorum* or *P. minor* (Appendix S2).

The ML trees of the *COXIF* and *Cytb* datasets (Figures 4A, B) recovered different topologies. The monophyly of most species was well supported by BS and posterior probability (PP) values over 75 and 0.95, in phylogenetic trees of the major dataset (Figure 4). However, the monophyly of *P. liuorum* was either poorly supported by a low BS value of 28 in the ML tree or not indicated in the BI tree of the *COXIF* dataset (Figure 4A). The *COXIF* trees resolved *P. argenteus* as the outermost species sister to all of its congeners. *P. minor* was resolved as the second outermost species, but the support values of such a relationship were low (*COXIF*: BS = 52, PP = 1, Figure 4A). The *Cytb* trees resolved the sister relationship of *P. argenteus* and *P. minor* (BS = 52, PP = 0.97). Although the monophyly of *P. candidus*, *P. cinereus*, and *P. liuorum* was well supported in the *COXIF* and *Cytb* trees (*COXIF*: BS = 81, PP = 1; *Cytb*: BS = 100, PP = 0.99, Figures 4A, B), relationships of the three species were different in the phylogenetic trees. The *COXIF* tree resolved *P. liuorum* as the sister species of *P. candidus* (BS = 46, PP = 0.63, Figure 4A), but the *Cytb* tree recovered its closer relationship with *P. cinereus* (BS = 74, PP = 0.88, Figure 4B). *P. chinensis* was well supported as the sister species of *P. punctatissimus* (*COXIF*: BS = 91, PP = 1; *Cytb*: BS = 98, PP = 1, Figures 4A, B); these two species were sister species to *P. candidus*, *P. cinereus*, and *P. liuorum* (*COXIF*: BS = 54, PP = 1; *Cytb*: BS = 66, PP = 0.75). The phylogenetic relationship of the seven species in the MG trees was identical to that in the *Cytb* trees. The topologies of phylogenetic trees of the MG dataset mostly agreed with those of the *Cytb* trees. All nodes in the MG trees were well supported by BS and PP values of 100 and 1 (Figure 4C), respectively. Support values for the monophyly of *P. cinereus* and *P. candidus* were not available, as the two species have only one mitogenome. The ML tree of the reduced MG dataset showed completely identical relationships among the seven *Pampus* species to those in the MG dataset (Figure 5B), which was thus used as the input tree for divergence time inference in BEAST.

Most species delimitation analyses favored two solutions for operational taxonomic units (OTUs) within the genus *Pampus* (Figure 4): 1) in the five-OTU solution, *P. candidus*, *P. cinereus*, and *P. liuorum* were delimitated as a single OTU, with other species as different OTUs; 2) in the seven-OTU solution, all the seven species were considered as OTUs severally. The ASAP, bPTP, and GMYC of the *COXIF* datasets favored the five-OTU solution, while those of the *Cytb* dataset indicated the seven-OTU solution. For the MG dataset, the bPTP and GMYC agreed on the seven-OTU solution, but the ASAP on its gene partitions indicated different results (Figure 4C): 1) *ATP8*, *COXI*, *COXII*, and *COXIII* favored the five-OTU solution; 2) *Cytb*, *ND2–6*, and *ND4L* favored the seven-OTU solution; 3) *ATP6*, *P. candidus*, *P. cinereus*, and *P. liuorum* were delineated as different OTUs, but *P. chinensis* and *P. punctatissimus* were merged as a single OTU (i.e., six-OTU solution); 4) *ND1* postulated eight OTUs, and an MG sequence of *P. minor* (accession number, MH037007) was delineated as an additional OTU to the seven OTUs of the valid species.

## The distributions of the *Pampus* species

The sampling localities and correct identities of the mitochondrial sequences were annotated in Figure 3. The *COXIF* and *Cytb* datasets contained the highest number of

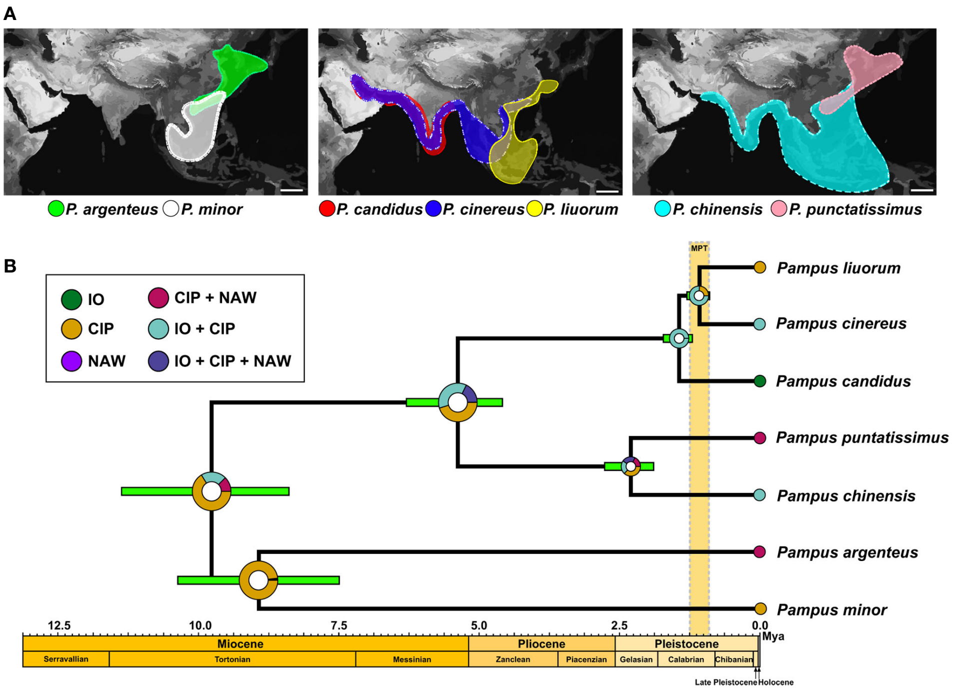

FIGURE 5
Divergence time inference and ancestral reconstruction of the seven *Pampus* species. **(A)** Distributions of each lineage of genus *Pampus* based on mitochondrial data; scale bars at lower-right corner of the maps indicate 1,000 km. **(B)** Divergence time inference and ancestral state reconstruction in BEAST v1.10.4 and RASP v4.2. IO, Indian Ocean; CIP, Central Indo-Pacific; NAW, Northeast Asian waters. The intervals of the geographic epochs are plotted based on Steinthorsdottir et al. (2021). The interval of the Mid-Pleistocene transition (MPT) is plotted based on Petrick et al. (2019).

sampling sites among the analyzed datasets (Table 1), while the sampling sites from other datasets were mostly included in those of the two datasets (Appendix S2). The distributions of the seven identified species were similar in both datasets. In brief, all the mitochondrial sequences of the genus *Pampus* derived from the Indo-West Pacific region, through the Arabian Gulf to coastal Japan (Figure 3). *P. argenteus* and *P. punctatissimus* were reported from Japan to the northern South China Sea. The distribution of *P. chinensis* extended from the Arabian Sea to the East China Sea, south to the Changjiang River estuary. *P. cinereus* was found through the Arabian Gulf (Bahrain and Kuwait, four specimens, Appendix S2) to the northern South China Sea. *P. candidus* were mostly found in the IO, from the Arabian Gulf to the Bay of Bengal, but occurrences of the species were sparsely reported in China and Malaysia. *P. liuorum* and *P. minor* were endemic to the CIP and not reported in the IO, with their westernmost sequences reported in the Malacca Strait (Figure 3). The distribution range of the genus *Pampus* encompassed three areas with obviously different species diversities, i.e., the IO (hosted three species, *P. candidus*, *P. chinensis*, and *P. cinereus*), the CIP (hosted six species, *P. argenteus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus*), and the NAW (hosted two species, *P. argenteus* and *P. punctatissimus*; Figure 3). The three areas were thus used as three states for analyses in RASP.

### Divergence time and ancestral distribution reconstruction

The mean calibrated substitution rate of *COXI* was 1.19%/million years (HPD95: 0.60–1.75%/million years). The tMRCA of the genus *Pampus* was 9.76 Mya (HPD95: 8.35–11.33 Mya). The divergence between *P. minor* and *P. argenteus* was dated back to 8.9 Mya (HPD95: 7.5–10.37 Mya). The tMRCA of *P. candidus*, *P. cinereus*, and *P. liuorum* was 1.46 Mya (HPD95: 1.20–1.72 Mya), and *P. liuorum* differentiated from *P. cinereus* at 1.07 Mya (HPD95: 0.88–1.28 Mya). The divergence time of *P. chinensis* and *P. punctatissimus* was 2.33 Mya (HPD95: 1.92–2.79 Mya), while the two species separated from *P. candidus*, *P. cinereus*, and *P. liuorum* in 5.4 Mya (HPD95: 4.57–6.28 Mya).

The Statistical Dispersal-Extinction-Cladogenesis model suggests three ancestral states for the most recent common ancestor (MRCA) of the genus *Pampus* (CIP, IO + CIP, and CIP + NAW), and the occurrence of these ranges was 66.18%, 21.34%, and 12.47%, respectively (Figure 5B). Therefore, it postulated a CIP origin for the genus *Pampus*. The MRCA of *P. argenteus* and *P. minor* was also assumed to distribute in CIP (98.24%), while the MRCA of *P. candidus*, *P. cinereus*, and *P. liuorum* might distribute in IO + CIP (99.75%, Figure 5B). The model also favored an IO + CIP (75.80%) origin for the MRCA of *P. liuorum* and *P. cinereus*. Although the MRCA of *P. punctatissimus* and *P. chinensis* had a higher probability (37.01%) for an IO + CIP origin, the probabilities for other states were also high and varied from 18.05% to 22.72% (Figure 5B).

## Discussion

### Global mitochondrial data provide new evidence for taxonomy of genus *Pampus*

Although a large number of mitochondrial sequences of the genus *Pampus* have been published today, only seven species could be delimitated (Table 1, Figure 4). It agrees with most conclusions of the recent mitochondrial studies, i.e., Li et al. (2019); Radhakrishnan et al. (2019); Wei et al. (2021), and Roul et al. (2021). In contrast, Yin et al. (2019), based on phylogenetic analyses with a large number of nuclear loci, proposed only five species within the genus *Pampus*. *P. liuorum* was synonymized with *P. cinereus* because the two species formed a mixed clade in the phylogenetic tree of Yin et al. (2019). However, it is questioned that the mixed clade of *P. liuorum* and *P. cinereus* in Yin et al. (2019) might actually contain three well-supported subclades, corresponding to three *Pampus* species (i.e., *P. candidus*, *P. cinereus* and *P. liuorum*, Wei et al., 2021; Roul et al., 2021). In our results, species delimitations with *COXIF* datasets and *ATP8*, *COXI*, *COXII*, and *COXIII* partitions of the MG dataset also delineate *P. candidus*, *P. cinereus*, and *P. liuorum* as a single OTU, which is different from most of the delimitation results (Figure 3). The ASAP of *ATP6* also delineates *P. chinensis* and *P. punctatissimus* as a single OTU, even though the two species are morphologically distinct (Li et al., 2019; Roul et al., 2021; Wei et al., 2021). Their conflicts with most of the delimitation results might be explained by a low level of differentiation among some species in these genes. For example, Wei et al. (2021) indicated that there is only 2–4 bp of difference between the *COXIF* sequences of *P. liuorum* and *P. cinereus*. The low levels of differentiation in these genes might affect the accuracy of species delimitations, and the congruences among different molecular markers should be accounted for. Based on most delimitation results, we conclude seven species in the genus *Pampus*, which, following Wei et al. (2021), are *P. argenteus*, *P. candidus*, *P. chinensis*, *P. cinereus*, *P. liuorum*, *P. minor*, and *P. punctatissimus* (Figure 2).

Many studies (e.g., Liu et al., 2013a; Li et al., 2017; Li et al., 2019) hypothesized *P. echinogaster* and *P. argenteus* as two species despite their morphological similarities (e.g., see comparisons in Liu et al., 2013a), which overlook their different distributions recorded by earlier works (e.g., Haedrich, 1967; Lindberg and Krasyukova, 1989; Nakabo, 2002). Our results clearly indicated that *P. argenteus* redescribed by Liu et al. (2013a) was widely distributed through the northern South China Sea to the Bohai Sea and coastal Japan (Figure 3), and all the sequences previously noted as *P. echinogaster* (e.g., Li et al., 2017) were confidently identified as *P. argenteus* (Figure 4; Appendix S2). Furthermore, the validity of *P. echinogaster* proposed by Li et al. (2017) was based on its genetic difference with *P. argenteus sensu* Li et al. (2013), whereas the latter was identified as *P. candidus* in our analysis (Figure 4; Appendix S2). Therefore, the validity of *P. echinogaster* proposed by Li et al. (2017) is incorrect and based on comparisons with misidentified "*P. argenteus*". In addition, only *P. punctatissimus* and *P. argenteus* were found inhabiting the type locality of *P. echinogaster* (i.e., the Bohai Sea, Figure 3), supporting that *P. echinogaster* should be either of these two species. Given that *P. echinogaster* has been frequently used to represent northern populations of *P. argenteus* (e.g., Liu et al., 2013a; Li et al., 2017), we propose the species as a junior synonym of *P. argenteus*.

*P. cinereus* was frequently reported in several Chinese waters (e.g., Liu et al., 2002; Cui et al., 2010; Li et al., 2019), but "*P. cinereus*" found in China actually contains two different species. Due to the loss of type specimen, a neotype is designated for *P. cinereus*, and *P. liuorum* is proposed to represent the other "*P. cinereus*" in China (Liu et al., 2013b; Liu and Li, 2013). The validities of the two species have been confirmed by Wei et al. (2021). Roul et al. (2021) assumed that *P. cinereus* was endemic to West Pacific and resurrected *P. griseus*, which dominates the Bay of Bengal. Nevertheless, *P. griseus* and *P. cinereus sensu* Roul et al. (2021) were identified as *P. cinereus* and *P. liuorum* in our results, respectively (Figure 3; Appendix S2), so the resurrection of *P. griseus* was incorrect due to the misidentification of *P. cinereus* and *P. liuorum*. We uncovered that *P. cinereus* has a broader distribution in the IO and CIP, which also refuted the suggestion of Roul et al. (2021) on the distribution of *P. cinereus*. Although the exact type locality of *P. cinereus* was not given in Bloch (1795), the types of *P. cinereus* might in fact come from waters around India. Bloch (1795) quoted Mr. Christoph Samuel John's words that the local people made *karawade* with *P. cinereus*. The word *karawade* means dried fish in the Tamil language, which is spoken in Tamil Nadu (southern India). The specimen provider, Mr. John, had been based in Tranquebar (i.e., Tharangambadi, Tamil Nadu) since 1771 (Paepke, 1999), which was also stated as the only known habitat for *P. cinereus* in Bloch's later work, i.e., Bloch and Schneider (1801). Our result indicates that *P. cinereus* redescribed by Liu et al. (2013b) is broadly distributed through the Arabian Gulf to the South China Sea, whereas *P. liuorum* is not present in the Indian Ocean (Figure 3). Therefore, the neotype designation of *P. cinereus* by Liu et al. (2013b) appears appropriate, whereas *P. liuorum* should not be treated as *P. cinereus* due to its absence in the Indian Ocean (Figure 3).

*P. nozawae* (Ishikawa, 1904) was treated as valid species in several studies (e.g., Huang et al., 2016; Jawad and Liu, 2017; Hou et al., 2018). However, all the "*P. nozawae*" sequences were identified as either *P. cinereus* or *P. minor*, and none of them were collected from the type locality of *P. nozawae* (i.e., Hokkaido, Japan). Sequences of *P. argenteus* and *P. punctatissimus* have been reported from coastal Japan (Figure 4; Appendix S2), and only these two *Pampus* species have been persistently recorded in coastal Japan and Russia (e.g., Lindberg and Krasyukova, 1989; Nakabo, 2002). *P. argenteus* is a species with short dorsal and anal fin lobes (Liu et al., 2013a), while Ishikawa (1904) clearly stated those of *P. nozawae* "reaching to the base of caudal if laid backward". The description only suits the morphology of *P. punctatissimus* (Liu and Li, 1998b). Therefore, *P. nozawae* might be a synonym of *P. punctatissimus*. Nevertheless, the validity of *P. nozawae* could not be eliminated due to a lack of sequence data from coastal Japan and Russia (Figure 3).

## The origin and evolution of the genus *Pampus*

Our study revealed that the CIP is a biodiversity hotspot for the genus *Pampus*. Six of the seven valid species are co-distributed in the CIP region, whereas only three and two species inhabit the IO and NAW regions, respectively (Figure 3). The Indonesian–Australian Archipelago within the CIP hosts over 2,500 fish species (Parravicini et al., 2014; Maxwell et al., 2022) and has been implicated as the center of origin for many marine fish taxa (e.g., Lutjanidae, Rincon-Sandoval et al., 2020; Mulloidei, Santaquiteria et al., 2021). Our RASP analysis supports a CIP origin for the genus *Pampus* (Figure 5B), which agrees with the conclusion of Fan et al. (2022). The inference on divergence time dated tMRCA of the genus *Pampus* back to the late Miocene (Figure 5B; mean tMRCA: 9.76 Mya; HPD95: 8.35–11.33 Mya, Steinthorsdottir et al., 2021), which agrees with the late Miocene origins of many modern coral reef fish lineages in the Indonesian–Australian Archipelago (Renema et al., 2008; Bellwood et al., 2017; Steinthorsdottir et al., 2021). These results imply that the origin of the genus *Pampus* might be related to the development of the Indonesian–Australian Archipelago biodiversity hotspot. The distributions of *P. cinereus* and *P. liuorum* overlap near the Sunda Shelf (Figure 3), while Roul et al. (2021) proposed that the species separately dominates the Bay of Bengal and CIP. The divergences among *P. candidus*, *P. cinereus*, and *P. liuorum* were considered to be related to isolations by the Indian Subcontinent and Sunda Shelf (Sun et al., 2012; Fan et al., 2022). In this study, the divergence time of *P. cinereus* and *P. liuorum* (mean tMRCA: 1.07; HPD95: 0.88–1.28 Mya) fell in the Mid-Pleistocene transition (0.60–1.25 Mya, Figure 5B), a major transition in global climate (Petrick et al., 2019). The periodicity of the Earth's glacial-interglacial cycles shifted from 41,000 years to quasi-100,000 years at the Mid-Pleistocene transition, and the glaciations and resultant sea-level changes became more intensive and significant, which accounted for the weakening of the Indonesian Throughflow and exposure of the Sunda Shelf (Petrick et al., 2019). The channel at the Sunda Shelf that connects the populations in the Indian and Pacific Oceans was frequently interrupted during the successive sea level changes in the Pleistocene (Petrick et al., 2019), which is believed to cause trans-oceanic diversification of marine species between the IO and the western Pacific (Ahti et al., 2016; Waldrop et al., 2016; Fan et al., 2022). Therefore, the differentiation between *P. cinereus* and *P. liuorum* might be associated with the exposure of the Sunda Shelf during the glacial cooling at the Mid-Pleistocene transition.

## Merits and demerits of using global data to explore species diversity and distributions

In recent years, gene sequences of marine species are rapidly accumulating to meet the growing need for fishery management and environmental protection. Our analyses of these global sequence data revealed new boundaries of the distributions of the *Pampus* species. *P. argenteus* used to be considered widely distributed in the IO and CIP (Haedrich, 1967), only inhabiting waters from the northern South China Sea to coastal Japan (Figures 3, 5A). Roul et al. (2021) assume that *P. cinereus* (i.e., *P. griseus* of the study) is restricted to the Bay of Bengal and Southeast Asia, but our study indicates that the species is also presented in the Arabian Sea and Arabian Gulf (i.e., Bahrain, Kuwait, and Mumbai, eastern India, Figure 4). Specially, we collected fresh specimens of *P. cinereus* at landing sites of Bahrain and Kuwait (Figure 4), indicating that the species inhabits the Arabian Gulf (although not a common species here, L. A. Jawad, personal observation). Yamada et al. (1995) stated that *P. punctatissimus* is not distributed south to the Taiwan Strait, but numerous wild-caught *P. punctatissimus* and their sequences have been reported by Zhang and Hanner (2012) from the northern South China Sea (Figure 3; Appendix S2), which clearly rejects Yamada et al. (1995) statement. *P. punctatissimus* is actually a species widely distributed from the northern South China Sea (Figures 3, 5A) to coastal Japan and Russia (Lindberg and Krasyukova, 1989). Nevertheless, commercial transportation might sometimes affect the accuracy of global molecular data. Extra caution should be taken when dealing with sequences of commercial species. We questioned the presence of *P. candidus* in China reported by Li et al. (2013) because fresh or wild-caught specimens of this species have never been observed in coastal China (personal observation). In fact, China imports “silver pomfrets” (HS code: 03038930) from South Asian countries (e.g., India, Pakistan, and Myanmar, the Custom Statistics Database of China, http://43.248.49.97/). The exportation of *P. candidus* from India to China, the Middle East, and the EU was also reported by Roul et al. (2021). As a result, *P. candidus* can be found in fish markets across China (e.g., IOCAS000292 and IOCAS000293 of this study, purchased from a fish market in Qingdao, Appendix S2). The *P. candidus* specimens reported by Li et al. (2013) are likely import commodities sold in the fish markets of China. We also found a specimen of *P. candidus* in Pulau Perhentian, Malaysia (Figure 3, IOCAS000181), likely due to commercial transportation of the species from the Bay of Bengal to the eastern Malay Peninsula.

# Data availability statement

The data presented in the study are deposited in the NCBI Genbank, accession number OP035984–OP036119, OP066061–OP066192, OP096421–OP096425.

# Ethics statement

Ethical review and approval was not required for the animal study because the samples used in this study were dead specimens purchased from fish market and landing sites, which does not constitute any ethical issue with alive animals.

# Author contributions

JW, JL, and KX conceived the research. JW, JL, RW, LJ, KL, and YW conducted the sampling collection. JW, RW, YX, AH-U, KL, and YW performed the laboratory work. JW, RW, and YX performed data curation and analyses. JW wrote the original draft. KX and JL led the review and editing of the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note

## Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1050386/full#supplementary-material

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