



Postulating the Modality of Integrative Taxonomy in Describing the Cryptic Congener *Pampus griseus* (Cuvier) and Systematics of the Genus *Pampus* (Perciformes: Stromateidae)

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Pomfrets (genus *Pampus*), a highly commercial fishery resource distributed in the Indo-Western Pacific that includes Lessepsian migrants, have witnessed a series of systematic reforms. In this study, based on comprehensive sampling spanning type localities and coevals in the Northern Indian Ocean, the cryptic and valid species *Stromateus griseus* is resurrected from the synonymy and re-described as *Pampus griseus* (New Combination) based on 35 specimens from the Bay of Bengal, corroborated by a molecular analysis, which indicated a confined distribution of the species. The Bayesian phylogeny of the genus was reconstructed, incorporating redressed barcodes (582 nucleotides) and concatenated mitochondrial gene sequence data (1,822 nucleotides) generated from the recorded species *P. candidus*, *P. chinensis* and the neophyte along with sequences from GenBank entrusting the latest literature. The phylograms differed in topology as for seven valid species, and the one predicated on the concatenated data erected a highly supported polytomous clade for the *P. cinereus* complex (*P. griseus*, *P. cinereus*, and *P. candidus*) which shares synapomorphies. *Pampus argenteus* and *P. minor*, together, formed a sister clade to the rest. Climate-driven vicariant events during glacial epochs and the Indo-Pacific Barrier effect can be the drivers behind the Indian and Pacific Ocean sister lineages in *P. chinensis*. A multivariate analysis isolated the cryptic species from its congeners. This article portrays the systematics revision of genus *Pampus* with an integrative taxonomic approach compiling distinctive molecular, morphological, and anatomical features, revised key for species identification, taxonomic archives of Indian stromateids, and winds up with specific remarks.

Keywords: Bay of Bengal, phylogenetic trees, species delimitation, multivariate analysis, sagittal otolith, integrative taxonomy

INTRODUCTION

The genus *Pampus* (family: Stromateidae), commonly known as pomfret, first proposed by Bonaparte (1837), characterized by an oval to diamond-shaped body, falcate median fins with a series of 5–10 small blade-like spines protruding ahead of it, and absence of ventral spine on the pelvic bone (Haedrich, 1967), is widely distributed in the Indo-Western Pacific Oceans renowned for species diversity (Manel et al., 2020), with possible Lessepsian migrants in the Mediterranean (Sami et al., 2014). These medium-sized schooling fishes, at times invading estuaries and frequently caught in trawls (Haedrich, 1984; Last, 1997), are recognized as one of the most valuable and relished table fishes in both internal and export markets because of their soft and tender flesh, few bones, good taste, high protein and fat content (Gupta, 2020). There are reports on their utilization in Chinese medicines (Tang, 1987). High value and perpetual demand make the genus one of the most sought after in commercial targeted fisheries in its native ranges, such as India (CMFRI, 2020),¹ countries bordering the seas of China, the maritime subregion of the Bay of Bengal (“BOB”), Persian Gulf countries, and Pakistan (Froese and Pauly, 2020). Despite this, the taxonomy of the genus *Pampus* has been uncertain and is still debated because of synapomorphies (Yin et al., 2019), and, conversely, the taxonomic literature hinted that many of the known species probably represented misidentified ones, leading to the occurrence of synonyms (Li et al., 2019c).

Latest global reports indicate the presence of the following seven valid species in the genus including the cryptic species described herein: *Pampus argenteus*, *Pampus minor*, *Pampus punctatissimus*, *Pampus chinensis*, *Pampus cinereus*, *Pampus candidus*, and *Pampus* sp. In 2017, Jawad and Jig, based on detailed comparative osteology of the axial skeleton, identified eight valid species in this genus, such as *Pampus liuorum* (Liu and Li, 2013) and *Pampus nozawae* (Ishikawa, 1904), which were found to be invalid by previous and subsequent researchers who considered them as synonyms of *P. cinereus* (Liu et al., 2013a; Li et al., 2019c; Yin et al., 2019). The existence of a strong geographic genetic structure in *P. argenteus* from the Indo-Western Pacific area was indicated (Sun et al., 2013), and a COI-based analysis of *Pampus* specimens by Divya et al. (2017) revealed the presence of seven distinct but taxonomically indecisive clades with two putative species viz. *Pampus* sp.¹ from the Arabian Sea and the BOB, and *Pampus* sp.² from the BOB. Subsequently, the *Pampus* sp.¹ was re-described as *P. candidus* by Divya et al. (2019). They hinted that the *Pampus* sp.² is a second valid species that was previously designated as *Pampus* sp. nov by Li et al. (2016), and recommended further morphological investigation to arrive at a taxonomic conclusion. Later, Li et al. (2019c) reiterated seven species in the genus based on COI analysis and prepared a key for six, although it turned out to be inconclusive. In the same year, Yin et al. (2019) provided a robust classification of *Pampus* based on ample nuclear markers and detailed morphological re-examination that provided a simplified identification key for the following five species: *P. argenteus*, *P. punctatissimus*, *P. chinensis*, *P. minor*, and *P. cinereus*. Their study confirmed that *P.*

argenteus and *P. cinereus* are two distinct species and that *Pampus echinogaster* and *Pampus liuorum* are invalid being synonyms of *P. argenteus* and *P. cinereus*, respectively. They considered the three clades in *P. cinereus* that were grouped according to sampling localities as the *P. cinereus* complex.

Historically, five species of pomfrets (*Pampus*) were described from Indian waters in Cuvier and Valenciennes (1833): *Stromateus candidus* from Malabar (Kerala) and Pondicherry (Puducherry), *Stromateus securifer* from Bombay (Mumbai), *Stromateus griseus* from Pondicherry, and *Stromateus albus* and *Stromateus atous* from Visakhapatnam. The last two were synonymized to *P. chinensis* by Haedrich (1967). Later, *S. candidus*, in synonymy with *P. argenteus*, was resurrected to *Pampus candidus* (Cuvier, in Cuvier and Valenciennes, 1833), and *S. securifer* was synonymized with it by Divya et al. (2019), who indicated that *P. candidus*, so far treated as *P. argenteus* in India, appears to be the most common species in Indian waters, and that the latter is totally absent along the Indian coastline. Divya et al. (2019) further indicated that the name *Pampus griseus* (Cuvier and Valenciennes, 1833) is valid if the BOB counterpart (*Pampus* sp.²) turns to be distinct.

Inaccurate identification of cryptic fish species and use of ambiguous names in landing reports will lead to undesired consequences in long-term sustainable fishery management plans (Fischer, 2013), where collection of species-specific information is vital. Meanwhile, similarity in external morphological traits among pomfrets, in general, poses problems in proper identification, resulting in numerous controversies regarding species classification, associated nomenclatures, and numerous erroneous GenBank records (Li et al., 2019c). *Pampus candidus*, misidentified as *P. argenteus*, formed a regular export commodity from Veraval, a major port in India, to Chinese, Middle East, and EU markets, with reports of 10–15 containers (~26 tons/container) during peak fishing season (September to December) (Source: Export Inspection Council, Veraval). Precise information on species forms the basis for international trade, consumer safety, biodiversity research, and prevention of fraudulence (Fischer, 2013). Traceability is being applied within seafood supply chains to ensure the legality and sustainability of products (Lewis and Boyle, 2017). However, conventional fish identification methods based on morphology may, at times, lead to misidentification, especially in the case of cryptic and recently diverged species. Furthermore, this cannot be fully relied on when only a part of the body is available; therefore, mislabeling can happen at any point (Willette et al., 2017). In such situations, DNA-based approaches can be successfully applied as an alternative tool for seafood authentication, even on partially or fully processed fishes when important morphological characters are lost.

Traditional taxonomic tools cannot provide a stand-alone platform to solve the taxonomic perplexity of pomfrets; hence, an integrative taxonomic approach that combines molecular, morphological, and ecological characters, which is successful in detecting cryptic species (Guimarães et al., 2020) and resolving the systematics (Katwate et al., 2020), was adopted. This study aimed at the following objectives, viz., (i) establish the identity of the cryptic congener hitherto indicated in the literature as

¹<https://www.zauba.com/export{-}frozen+pomfret+fish-hs-code.html>

Pampus sp. nov (Li et al., 2016)/*Pampus* sp.² (Divya et al., 2017, 2019)/*Pampus* sp. (Li et al., 2019c) in comparison with its contemporaries *P. candidus* and *P. chinensis* sympatric in Indian waters (ii) re-evaluate *Pampus* spp. of the Indo-Western Pacific for phylogenetic resolution (iii) revise the systematics, and (iv) prepare a field identification key for all the species. Classical taxonomic tools, viz., morphology, multivariate analysis, gill raker shape, sagittal otolith morphology, vertebral count, morphology of transverse occipital canal of the lateral line, and fishery information, have been integrated into this study with molecular data for all the species fished along the Indian coast, and with global literature and database for inference.

MATERIALS AND METHODS

Taxon Sampling

One hundred thirteen fresh specimens of *Pampus* spp. were collected from various locations such as type localities along the east coast in the BOB (West Bengal, Odisha, Andhra Pradesh, and Tamil Nadu) and the west coast (Gujarat and Kerala) in the Arabian Sea from 2019 to 2020 (Figure 1). The specimens were sampled directly from fishing vessels and fish landing sites. The collected specimens were transported to the laboratory in crushed ice for detailed taxonomic investigation and photographed immediately to capture their original color and pigmentation. The species were tentatively identified based on original descriptions and recent keys (Divya et al., 2019; Li et al., 2019c; Yin et al., 2019).

Materials Examined

Pampus candidus/*Pampus* sp. (n = 69)

Six ex., 132–167 mm SL, Paradeep fishing harbor (20°17.345'N, 086°42.422'E), Jagatsingpur, Odisha, trawl, 40–70 m, sandy silt, 24 Jan. 2020; 9 ex., 117–177 mm SL, Atharabanki landing center (20°17'28.2264''N, 86°39'18.738''E), Jagatsingpur, Odisha, India, gillnet, 30 m, sandy silt, June 9 and October 3, 2020; 2 ex., 87–96 mm SL, Fort Kochi (9°58'6.1572''N, 76°14'35.6856''E), Kerala, gillnet, 10–15 m, muddy, June 29, 2020; 13 ex., 100–161 mm SL, Veraval fishing harbor (20°54'19.23''N, 070°22'52.03''E), Gujarat, gillnet, 30 m, muddy, July 14, 2020; 4 ex., 180–190.7 mm SL, Rameshwaram fish landing center (9.281146°N, 79.315055°E), Palk Bay, Tamil Nadu, trawl, 15–20 m, muddy, August 13, 2020; 7 ex., 70.6–120.5 mm SL, Puri north landing center (19°47'43.062''N, 85°49'38.5788''E), Puri, Odisha, shore seine, 3–5 m, sandy silt, August 18, 2019; 1 ex., 177 mm SL, Veraval fishing harbor (20°54'19.23''N, 070°22'52.03''E), Gujarat, trawl, 30 m, muddy, August 24 2020; 4 ex., 102–115 mm SL, Visakhapatnam Fishing Harbor (17.696°N, 83.301°E), Andhra Pradesh, trawl, 35–40 m, sandy silt, September 2, 2020; 7 ex., 130–203 mm SL, Nagapattinam fishing harbor (10°45'03.8''N, 79°50'24.0''E), Tamil Nadu, trawl, 30–100 m, rocky, September 11, 2020; 5 ex., 120–140 mm SL, Fish Market, Kochi, Kerala, India, September 7, 2020; 4 ex., 83–110 mm SL, Digha (21°36'58.3272''N, 87°29'56.8644''E), West Bengal, shore seine, 3.5 m, sandy silt, September 12, 2020; 2 ex., 146–150 mm SL, Kalamukku (9°59'18.006''N, 76°14'34.836''E),

Kochi, Kerala, trawl, 30–40 m, muddy, September 15, 2020; 2 ex., 150–170 mm SL, Puducherry (Pondicherry) fishing harbor (16°3'17.964''N, 78°14'47.49''E), trawl, sandy, Tamil Nadu, October 10, 2020; 3 ex., 150–170 mm SL, Cuddalore Harbor (11°42'52''N, 79°46'31''E), Tamil Nadu, Multiday trawl, 15 m, sandy, October 2020.

Pampus chinensis (n = 44)

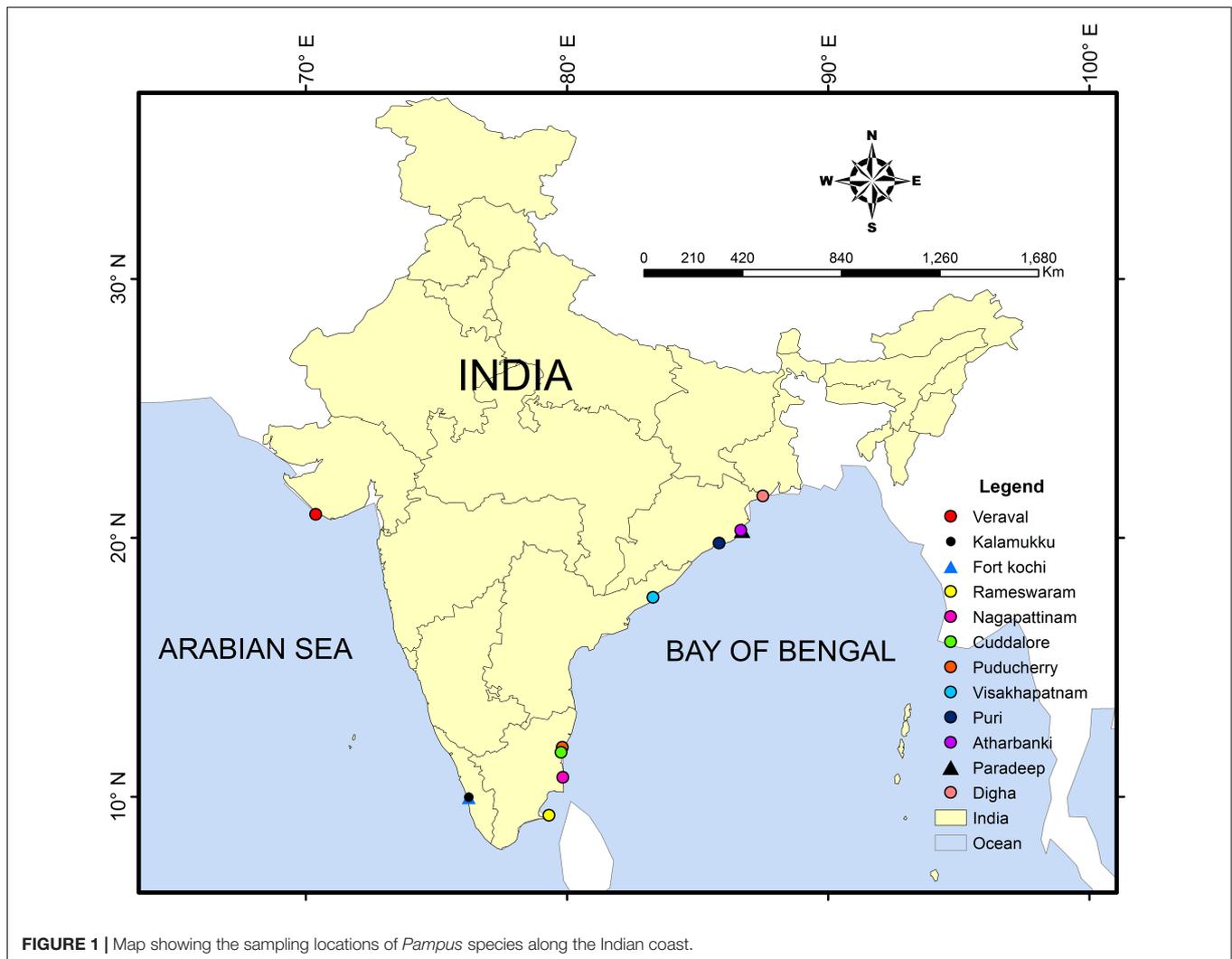
Five ex., 86–110 mm SL, Digha (21°36'58.3272''N, 87°29'56.8644''E), West Bengal, shore seine, 3.5 m, sandy silt, September 12, 2020; 6 ex., 87.2–152.5 mm SL, Puri North landing center (19°47'43.062''N, 85°49'38.5788''E), Puri, Odisha, gillnet, 10–12 m, sandy silt, July 24, 2019; 14 ex., 67–216.3 mm SL, Paradeep fishing harbor (20°17.345'N, 086°42.422'E), Jagatsingpur, Odisha, India, trawl, 40–70 m, sandy silt, September 8, 2020; 3 ex., 114–129 mm SL, Visakhapatnam fishing harbor (17.696°N, 83.301°E), Andhra Pradesh, India, trawl, 35–40 m, sandy silt, September 2, 2020; 4 ex., 163–203 mm SL, Veraval fishing harbor (20°54'19.23''N, 070°22'52.03''E), Gujarat, India, trawl, 60–70 m, muddy, August 24, 2020; 7 ex., 132–252 mm SL, Nagapattinam fishing harbor (10°45'03.8''N, 79°50'24.0''E), Tamil Nadu, India, trawl, 30–100 m, rocky, September 11, 2020; 2 ex., 160–170 mm SL, Puducherry fishing harbor (16°3'17.964''N, 78°14'47.49''E), Tamil Nadu, India, trawl, October 2020; 3 ex., 200–210 mm SL, Cuddalore Harbor (11°42'52''N, 79°46'31''E), Tamil Nadu, Single day trawl, 9 m, sandy, October 2020.

Museum Specimens Examined

Two specimens of *Pampus* from the Marine Biodiversity Referral Museum of ICAR-Central Marine Fisheries Research Institute (CMFRI), Kerala, India, and two digital images of *Pampus* from the Museum National D'histoire Naturelle, Paris were examined (Supplementary Figure 1).

Polymerase Chain Reaction and Sequencing

Genomic DNA was extracted using the phenol-chloroform method from ethanol-preserved fin clips of specimens (65 nos) specified in materials examined. Later, an additional sample of 18 nos. were added to maintain a proper sample size (Supplementary Table 1). Partial fragments of the COI gene were amplified using universal primer pairs Fish F2 (5' TCGACTAATCATAAAGA TATCGGCAC 3') and Fish R2 (5' ACTTCAGGGTGACCGAAGAATCAGAA 3') (Ward et al., 2005). Cyt *b*, ATP6/8, and 16S rRNA genes were amplified using the universal primers L14724 (5' GACTTGAAAAACCACCGTTG 3') and H15915 (5' CTCC GATCTCCGGATTACAAGAC 3') (Xiao et al., 2001); ATP8. 2L8331 (5' AAA GCRTYRGCCTTTTAAGC 3'), and COIII.2H9236 (5' GTTAGTGGTCAKGGGCTTGGRTC 3') (Sivasundar et al., 2001); and 16 Sar (5' CGCCT GTTTATCAAAAACAT 3') and 16 Sbr (5' CCGGTC TGAAGTCAGATCACGT 3') primers (Palumbi et al., 1991). Polymerase chain reaction (PCR) amplifications were performed in 25 µl using TaKaRa Emerald Amp GT PCR Master Mix, primer pairs, and template DNA. The PCR profiles were as



follows: 4 min at 94°C for initial denaturation followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 50–55°C depending on the genes for 30 s, elongation at 72°C for 45 s, and a final extension at 72°C for 10 min. The amplified products were purified and sequenced. Complementary sequences were edited and assembled into consensus using BioEdit v7.1.9.

Confirmation of Nucleotide Sequences

Sequence similarities were determined using the NCBI nBLAST tool, and the haplotype data generated for COI, Cyt *b*, 16S rRNA, and ATPase 8/6 genes from this study were deposited in GenBank (**Supplementary Table 1**; accession numbers: MW422591–MW422604, MW421904–MW421919, MW343690–MW343704, MW366881–MW366888, MW419276–MW419288, MW337238–MW337245, MW343460–MW343467, MW332295–MW332304, MW260616–MW260617, MW343468–MW343475, MW447297, MW447300–MW447301, and MW456736). Representative sequences of the Cyt *b* (1,137 nucleotides (“nt”) and ATPase8/6 genes (835 nt) from previous population genetic studies (Sun et al., 2012;

Divya et al., 2015) were also reanalyzed integrating sequences from this study to affirm the genetic distinctness of the cryptic species.

Phylogenetic Trees and Genetic Divergence

Separate phylogenetic analyses were carried out with two data sets, i.e., concatenated mitochondrial sequences (1,822 nt; **Supplementary Table 2**) and curated COI barcodes alone (582 nt; **Supplementary Table 3**), because of global data availability. The veracity of COI sequences from GenBank was confirmed, and misidentifications were corrected as per the latest references. Consequently, representative COI haplotypes were sampled for all the six valid species and *Pampus* sp. distributed in the Indo-Pacific Oceans, giving due weightage to their type localities and geographical origins. For concatenation of the noncoding (16S rRNA) and coding (COI and Cyt *b*) mitochondrial sequences, data available either from the same individuals or complete mitogenome data were used. In absentia, sequences from the same geographic areas were pooled after validation. The

concatenation consisted of 470 nt of 16S, 582 nt of COI, and 770 nt of Cyt *b* with no introns or indels in the latter two. *Stromateus stellatus* from the paraphyletic genus *Stromateus* and the carangid *Parastromateus niger* were used as outgroups. The two datasets were separately aligned using Clustal W with a default setting in MEGA X (Kumar et al., 2018). The net genetic distance between species groups was also calculated in MEGA X under uniform rates using a Kimura two-parameter (K2P) model (Kimura, 1980) for 51 concatenated sequences eliminating *P. minor* 2, 4, 5, and 6 because of insufficient characters for the Cyt *b* region. Appropriate partition strategies and evolutionary models for each partition in concatenated data were selected with PartitionFinder v.1.1.1. A Bayesian analysis was implemented with MrBayes v.3.2 using the best model, i.e., GTR+G. The final consensus tree was visualized and edited in FigTree v.1.4.3.² A Generalized Mixed Yule Coalescent (GMYC) model (Pons et al., 2006; Fujisawa and Barraclough, 2013), used for species delimitation analysis of concatenated multilocus data (Luo et al., 2018), was created by uploading the trees generated in BEAST1.8.0 (Drummond et al., 2012) with default settings. The maximum credibility tree was used as input for GMYC analysis with the SPLITS package in R (Ezard et al., 2009; Fujisawa and Barraclough, 2013), and results were visualized with R v.3.5.2 (R Core Team, 2018).

Morphometry and Otolith Comparison

Morphometric measurements and meristic counts were recorded according to Haedrich (1967) and Liu et al. (2013a,b). Total vertebrae were counted as the number of precaudal plus the number of caudal vertebrae, including the urostyle from the X-radiographs according to Jawad and Jig (2017). Sex and the gonad maturity stage of the specimens were determined to the possible extent based on the macroscopic observation of the gonads. The morphometric characters measured using a digital Vernier caliper (0.1 mm accuracy) were given as percentages of standard length (SL) for size-independent comparison with the other available species under this genus (Table 1). To remove the size component from the shape component, the morphometric measurements were subjected to allometric transformation, as suggested by Elliott et al. (1995). The standardization function was:

$$M_s = M_o \left(\frac{SL_m}{SL_o} \right)^b$$

where M_s is the standardized morphometric variable, M_o is the observed variable, SL_m is the overall mean of the standard length (scaling variable), SL_o is the observed standard length, and b is the within-group (here species) regression slope of Log M_o (Y-axis) on Log SL_o (X-axis). The transformed data were subjected to principal component analysis (PCA) using the FactoMinerR package in R v.3.5.2 (R Core Team, 2018). Sagittal otoliths were extracted, cleaned in distilled water to remove the dirt and remnant tissue, air-dried, and stored in plastic vials. Images of the medial face of the otoliths were captured using a stereomicroscope (Nikon SMZ1270) fitted with a camera. As both the otoliths were found symmetrical in shape and size, only the left otoliths were photographed and

TABLE 1 | Morphometric and meristic data for *Pampus griseus*, *Pampus candidus*, and *Pampus chinensis* from Indian waters.

Specimen	<i>Pampus griseus</i>	<i>Pampus candidus</i>	<i>Pampus candidus</i>	<i>Pampus chinensis</i>
	Present study	Divya et al., 2019	Present study	Present study
	<i>n</i> = 35	<i>n</i> = 28	<i>n</i> = 34	<i>n</i> = 44
Counts				
Dorsal fin rays	VIII–IX, 38–42	VII–IX, 40–42	VII–X, 36–42	41–49
Anal fin rays	V–VII, 36–39	V–VII, 36–41	V–VI, 36–40	38–45
Pectoral fin rays	22–26	22–24	22–28	20–27
Caudal fin rays	22–26	22–24	22–28	18–28
Gill rakers (total)	1–2 + 7–9 (8–11)	1–2 + 6–8 (8–10)	1–2 + 7–9 (9–11)	1–4 + 8–11 (9–14)
Total vertebrae	35–36	37	36–38	32–33
Measurements				
Standard length (mm)	71–178	78–133	87–203	67–252
Measurements (% SL)				
Maximum body depth (BD)	66.9–84.0	63–76	60.6–83.3	62.7–88.5
Dorsal fin length (DFL)	37.4–56.2	26–40	33.5–45.2	35.3–60.3
Anal fin length (AFL)	54.9–110.5	30–55	60.6–79.3	32.5–62.0
Pectoral fin length (PFL)	35.1–49.6	39–51	38.2–46.2	28.6–51.0
Caudal fin length (CFL)	62.0–132.0	39–76	63.8–95.3	25.9–47.9
Predorsal distance (PDD)	39.9–50.7	51–58.4	44.0–60.5	26.4–61.4
Preanal distance (PAD)	48.7–58.9	49.2–61.2	43.6–64.3	34.2–64.2
Length of the dorsal fin base (DFBL)	51.8–57.3	47.37–56	46.9–56.7	52.0–71.1
Length of the anal base (AFBL)	51.1–58.8	47–57.5	49.6–59.2	52.5–66.4
Caudal peduncle length (CPL)	4.7–12.9	8.87–14.6	6.8–10.0	4.0–9.9
Caudal peduncle depth (CPD)	5.0–12.9	9.1–12.6	6.9–12.7	11.6–17.0
Head length (HL)	24.5–31.3	25.3–31.2	22.0–30.4	23.0–33.0
Measurements (% HL)				
Snout length (SNL)	21.3–31.0	23–31.7	22.2–32.3	20.0–33.3
Inter-orbital width (IOL)	40.9–49.2	40.5–47.3	36.3–51.5	42.7–64.1
Eye diameter (ED)	21.6–32.3	23–31	20.5–31.6	14.8–23.6
Length of upper jaw (LUJ)	20.7–32.8	26.5–32.4	21.2–33.3	24.4–35.9

Standard length is expressed in mm; measurements are expressed as percentage of standard length and head length.

²<http://tree.bio.ed.ac.uk/software/figtree/>

used for comparison. The otoliths were assessed and compared based on gross morphology following Zhang et al. (2017). The key characteristics, like overall shape, presence/absence of crenulations, shape of anterior and posterior regions, type and shape of sulcus, ostium, and cauda, were compared across species for similarity or dissimilarity. Furthermore, we have also collected otoliths across different size ranges (juvenile, subadult, and adult) to account for any ontogenetic changes as the species grows in size, which was lacking in descriptions of Zhang et al. (2017). Voucher specimens of whole fish of each species were fixed in 10% formalin, transferred to 70% ethanol, and then stored for future reference.

RESULTS AND DISCUSSION

Nucleotide Sequence Characteristics

Three species, *viz.*, *P. chinensis*, *P. candidus*, and *Pampus* sp., were identified based on BLAST results and further curated with the latest literature. *P. chinensis* does not pose a problem in detection and showed >99% identity with NCBI sequences, while morphological similarity of the other two species necessitated the assistance of COI barcodes for identification. The Indian Ocean representatives of *P. chinensis* followed a pattern similar to that of previous submissions from the Arabian Sea (FJ226529–FJ226530; KP410329) and exhibited a COI divergence of 0.6–1% from the Pacific. The COI data generated from this study and previous ones were summarized for analysis in **Supplementary Table 3**. Barcodes of the cryptic species exhibited a complete identity with records from the BOB sub-region in South Asia covering North-eastern Indian Ocean (KF373011–KF373012 and KX530942–KX53094), Bangladesh (KX455908), Myanmar (DQ107597–DQ107598 and DQ107600), Myanmar and Thailand (JN202078–JN202087 and JN202090–JN202092), and Vietnam (DQ107599). The Cyt *b* sequences of the same showed >99.7% similarity with sequences from BOB populations of Thailand and Burma (JF790230–790250) submitted by Sun et al. (2012), while ATPase showed a ~100% identity with the sequences (JX293029–JX293030) submitted by Divya et al. (2015) from West Bengal, India. Thus, the COI barcodes and other gene sequences implied that *Pampus* sp. may be the *Pampus griseus* indicated by Divya et al. (2019). Review of Cyt *b* data from the Indo-Pacific (Sun et al., 2012) and ATPase 8/6 gene data (**Supplementary Table 4**; Divya et al., 2015) indicated K2P divergence values of 3.86% and 5.3%, respectively, between *P. candidus* and *P. griseus* (**Supplementary Figures 2, 3**).

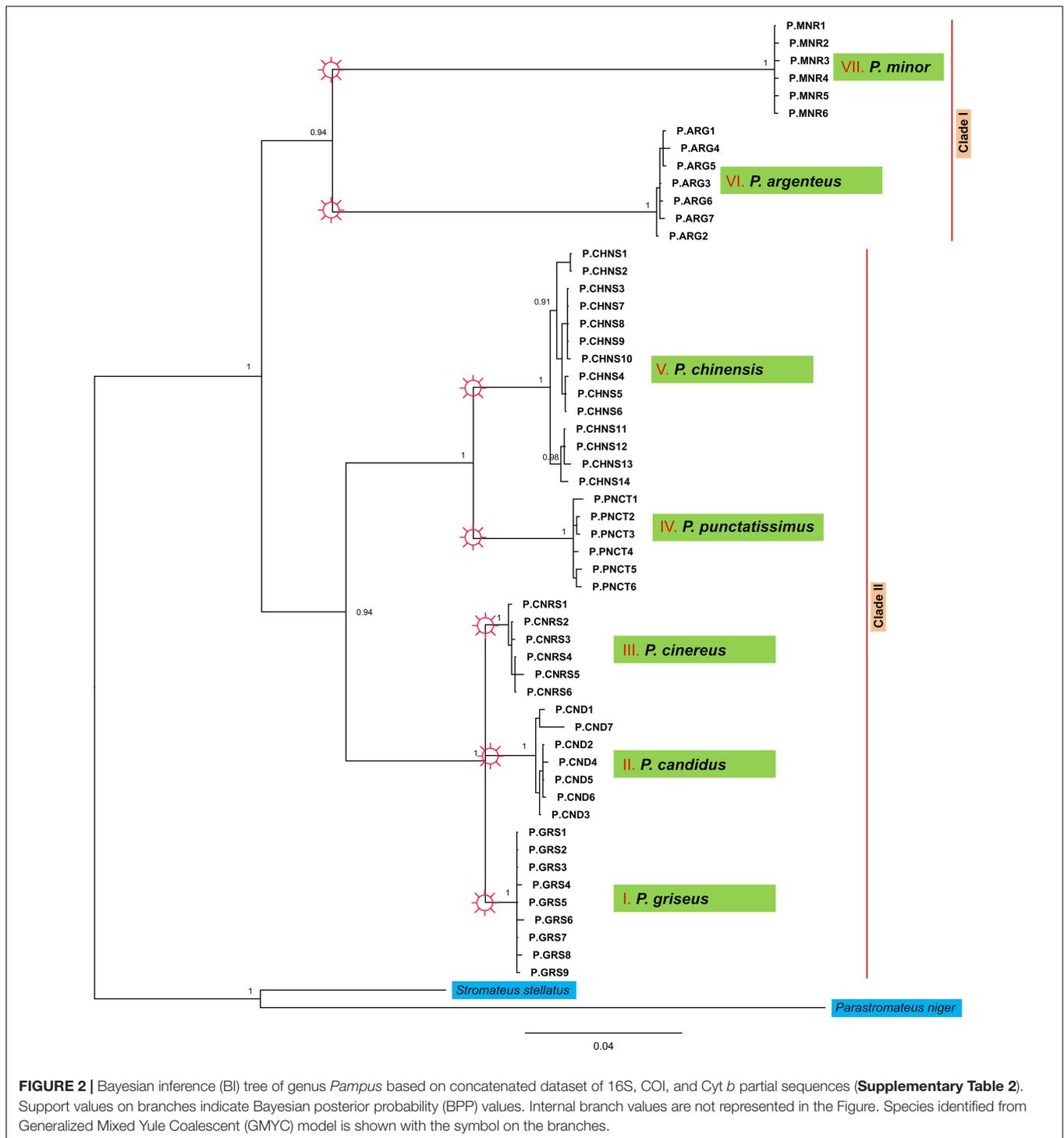
Phylogenetic Interrelationships Among *Pampus* Species

Although there is an overall similarity, conflicts could be noted in the tree topologies derived from BI analyses of the two data sets (**Figure 2** and **Supplementary Figure 4**), which visualized seven monophyletic clades representing seven species. However, a Bayesian Inference (BI) tree derived from concatenated nucleotide data supported the major clades with high posterior probability values (BI PP > 0.95). Hence, discussions are mainly based on the BI tree (**Figure 2**) derived from the concatenated data unless otherwise stated. In this phylogram, one major clade

contained the sister groups *P. argenteus* and *P. minor*. The second major clade had two sub-clades in which *P. chinensis* and *P. punctatissimus* formed sister groups to each other in one clade, whereas *P. griseus*, *P. candidus* and *P. cinereus* grouped in another clade. *P. chinensis* bifurcated into two representing the Pacific and Indian Ocean lineages. Interestingly, the haplotypes at Veraval were unique and were not shared with any other region. The net evolutionary divergence value between the two major clades was 8.1%, while it was 6.9% between the sister clades of the second major clade. The intraspecific divergence ranged from 0 to 0.009, and inter-specific genetic distance spanned from 1.6 to 15.5% (**Table 2**). The major clades were not well-defined in the COI-based species tree (**Supplementary Figure 4**), particularly with reference to *P. minor* and *P. argenteus*.

Bayesian analysis of phylogenetic interrelationships based on the concatenated gene tree proved to give a stable output compared to the previous individual gene genealogy with differing topologies (Cui et al., 2010, 2011; Divya et al., 2017). From our study, *P. cinereus* and *P. griseus* do not form a separate cluster in the BI trees and lead to polytomy unlike previous phylograms (Li et al., 2019c; Yin et al., 2019). The NJ tree in Li et al. (2019c), which is concordant with the COI-based tree in this study, received a comparatively low Bayesian probability value in this node, probably because of the insufficient character sampling in single-gene trees. The overall tree topology derived from the concatenated data matches with the robust gene tree built on the conserved nuclear coding markers outlined in Yin et al. (2019) but differs in the clustering of species in the *P. cinereus* complex which does not include exact species designations. Phylograms from previous studies indicating exact species designations (highlighted) based on results from our study incorporating latest revisions (Divya et al., 2019; Yin et al., 2019) are given in **Supplementary Figure 5**. The species delimitation analysis indicated the occurrence of nine taxonomic units with two morphospecies (*P. chinensis* and *P. candidus*) subdivided into two GMYC species (**Supplementary Figure 6**). The maximum intraspecific K2P distance in the concatenated data (51 sequences) was 0.7% while the minimum intergroup distance was 1.6% (**Supplementary Table 5**). Hence, the two GMYC units in *P. chinensis* and *P. candidus* that differ by 0.7% should be considered as the same species, thus setting up only seven independently evolving species in the genus.

The integrated data in this study, although discordant with the assumption of a possible species complex in *P. chinensis* (Divya et al., 2017; Li et al., 2019c), support the existence of heterogeneous populations forming a vicariant sister lineage pair in the Indo-Pacific Oceans. The lineage observed in *P. chinensis* in this study supports previous findings by Li et al. (2019a) who hypothesized the lack of genetic admixture of refuge populations of the Pacific and Indian Ocean to the geographic barrier, the Malay Peninsula, a part of Sundaland during past glacial periods (Hall and Morley, 2004). The effect of the Indo-Pacific Barrier resulted in a curbed gene flow that became prominent during Pleistocene sea-level variations, resulting in the sympatric distribution of ichthyofaunal lineages in the Indian and Pacific Oceans (Gaither and Rocha, 2013). The presence of non-shared haplotypes in Veraval indicates the probability of a distinct genetic stock in *P. chinensis*. Although there are reports



of another lineage in *P. minor* from Malaysia (Li et al., 2019b), we could not include representative sequences in genetic distance calculation because of unavailability of data. The genetic distance values in this study lie in the range reported by Li et al. (2019c) with a comparatively higher divergence and bootstrap support in the *P. cinereus*–*P. griseus*–*P. candidus* complex. The evolutionary history of the recently diverged species may be the probable cause for the <2% heuristic threshold divergence (1.6%) between

P. cinereus and *P. griseus*, as suggested by Divya et al. (2017). However, this value is higher compared to the single gene-based phylogenetic inference (Divya et al., 2017; Li et al., 2019c), indicating the efficiency of multilocus-based gene trees.

Our results agree that the *Pampus* sp. collected from the Indian Ocean by Divya et al. (2017) was closely related to the *P. cinereus* redescribed by Liu et al. (2013a) from China. The clustering of the three sister species, *P. griseus*, *P. candidus*, and *P. cinereus*

TABLE 2 | Genetic distance based on K2P model (Kimura, 1980) among the seven species of *Pampus* in the Indo-Western Pacific Oceans based on the concatenated data (1,822 nt).

		1	2	3	4	5	6
1	<i>Pampus griseus</i>	–					
2	<i>Pampus cinereus</i>	0.016	–				
3	<i>Pampus candidus</i>	0.023	0.022	–			
4	<i>Pampus chinensis</i>	0.085	0.084	0.083	–		
5	<i>Pampus punctatissimus</i>	0.089	0.086	0.089	0.046	–	
6	<i>Pampus argenteus</i>	0.135	0.132	0.134	0.132	0.137	–
7	<i>Pampus minor</i>	0.152	0.146	0.148	0.148	0.154	0.155

indicated a convergent evolution characterized by the elongation of dorsal, caudal, and anal fins, a shared characteristic among the three (Yin et al., 2019). The tree topology discriminated each species into separate clades with no shared haplotypes, concordant to observed morphological divergence.

Multivariate Comparison of *Pampus* Species From India

Multivariate analysis has been widely performed for species identification and discrimination (Takacs, 2012;

Marramà and Kriwet, 2017; Behera et al., 2020). The first three principal components or dimensions accounted for 71.7% of the variability in the data as reflected by the eigenvalues of the principal components. The first principal component (Dim 1) separates the species *P. chinensis* from the two other species (*P. griseus* and *P. candidus*). Morphometric variables, such as caudal fin length (CFL), anal fin length (AFL), length of the dorsal fin base (DFBL), length of the anal fin base (AFBL), inter-orbital width (IOL), and length of upper jaw (LUJ) were found to have significantly higher loadings on the PC1 or Dim 1 and, hence, have higher discrimination power in the separation of *P. chinensis* from the other two species. The other two closely resembling species, *P. griseus* and *P. candidus*, showed a significant overlap and were not separated along PC1. The second dimension (PC2 or Dim 2) was able to achieve significant separation from these two species in a multivariate space with some overlap. Morphometric variables, such as caudal peduncle length (CPL), pre-dorsal distance (PDD), pectoral fin length (PFL), and eye diameter (ED), were important morphometric measurements capable of separating *P. candidus* and *P. griseus* (Figure 3). The marginal overlap in the two groups suggested their cryptic nature and, hence, is misidentified as single species (*P. candidus*) until now.

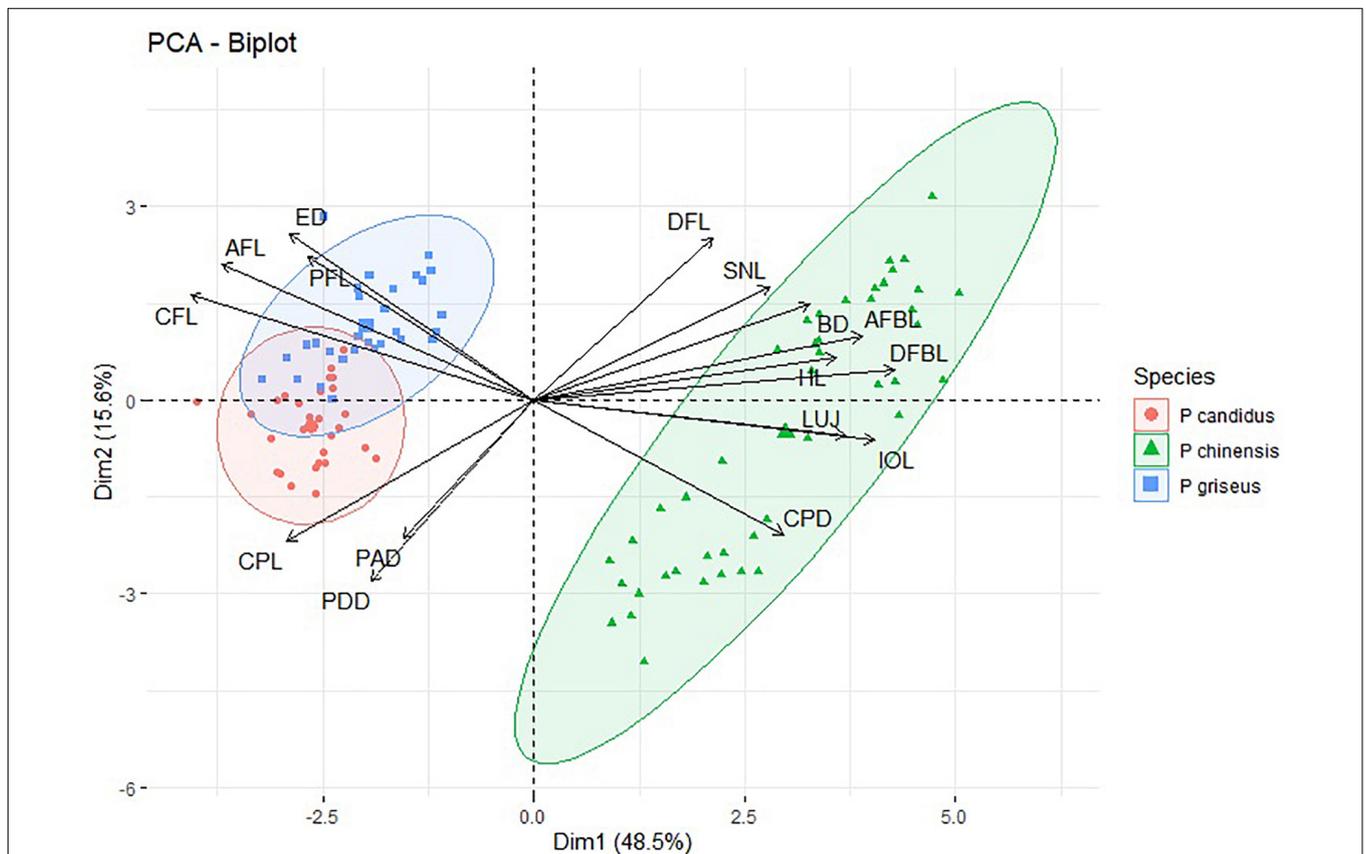


FIGURE 3 | Bi-plot showing the variables and individuals (samples) oriented along the first two principal components with eclipses (species). The Dim1 and Dim2 are the first and second principal component extracted in PCA and the notation in graphs refers to the morphometric variables mentioned in Table 1.

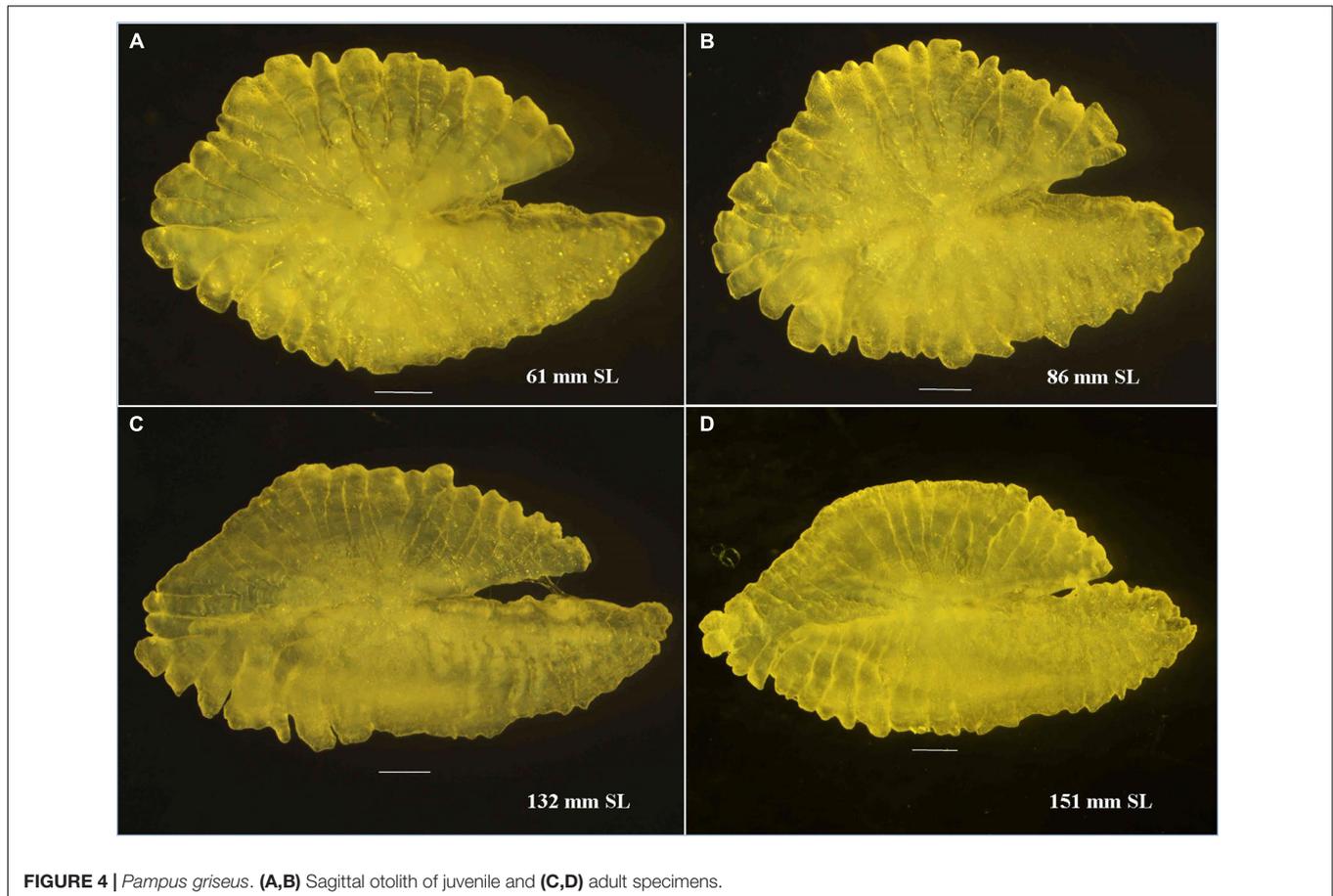


FIGURE 4 | *Pampus griseus*. (A,B) Sagittal otolith of juvenile and (C,D) adult specimens.

Thus, by molecular and multivariate analyses, it is concluded that the specimens in the materials examined (*P. candidus*/*Pampus* sp.) collected from Kerala, Veraval (Gujarat), Rameshwaram (Tamil Nadu), and Nagapattinam (Tamil Nadu) represented *P. candidus*, while the rest of the samples were of *P. griseus*.

Comparison of Otoliths

Otoliths are depicted to have high morphological variability with particular characteristics across species and genera (Koken, 1884; Platt and Popper, 1981), and such species-specific characteristics have been introduced in taxonomy (Schmidt, 1969; Nolf, 1985). The sagittal otolith morphology of five *Pampus* species from the Chinese coast was described by Zhang et al. (2017). The *Pampus* sp. mentioned in their study can be *P. argenteus* or *P. echinogaster*, which are currently synonymized to *P. argenteus* (Yin et al., 2019). A comparison of the sagittal otolith morphology of seven valid species of *Pampus*, such as *P. griseus* (Figure 4), *P. candidus* (Figure 5), and *P. chinensis* (Figure 6), from Indian waters, and four species from Chinese waters (Table 3 and Supplementary Figure 7) revealed that the overall gross morphology of the sagittal otolith of *P. griseus* is more similar to that of *P. candidus*, *P. cinereus*, *P. chinensis*, and *P. punctatissimus* than that of the others (see Figure 2 in Zhang et al., 2017). Furthermore, the subtle variations across different size ranges (as observed

in this study) reduce its taxonomic utility to differentiate *P. griseus* from closely resembling congeneric species, especially when used exclusively.

Revision of Systematics

Order Perciformes (Bleeker, 1863).

Family Stromateidae (Rafinesque, 1810).

Genus *Pampus* (Bonaparte, 1834).

Pampus cinereus Species Complex

In the *Pampus* genus, the first species complex, “*Pampus nozawae* species complex”, recognized by Cheng and Zheng (1987), consisted of *P. nozawae*, *P. punctatissimus*, and *P. cinereus*. Later, Liu and Li (2013) recognized another species complex, “*Pampus punctatissimus* species complex,” which included *P. punctatissimus*, *P. cinereus*, and *P. liuorum*. However, both these complexes, characterized by greatly extended anterior rays of the anal fin, were not approved by subsequent researchers. In the first complex, *P. nozawae*, described by Ishikawa (1904), was proved to be an invalid species that was synonymized with *P. punctatissimus* and *P. cinereus* (Yamada et al., 2007; Liu et al., 2013a). It is to be added that *P. nozawae*, reported by Huang et al. (2016), from Daya Bay, China indeed represents *P. cinereus*. Similarly, *P. liuorum* of the second species complex described

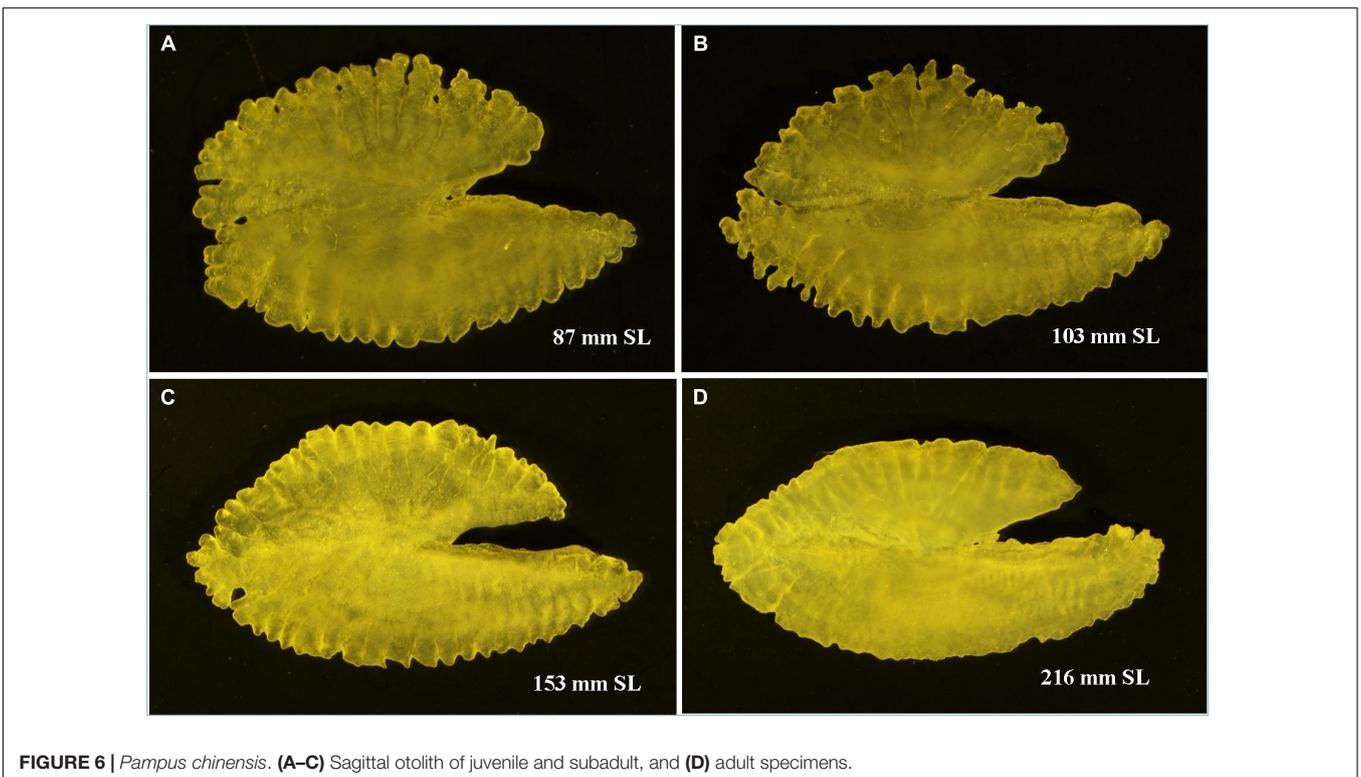
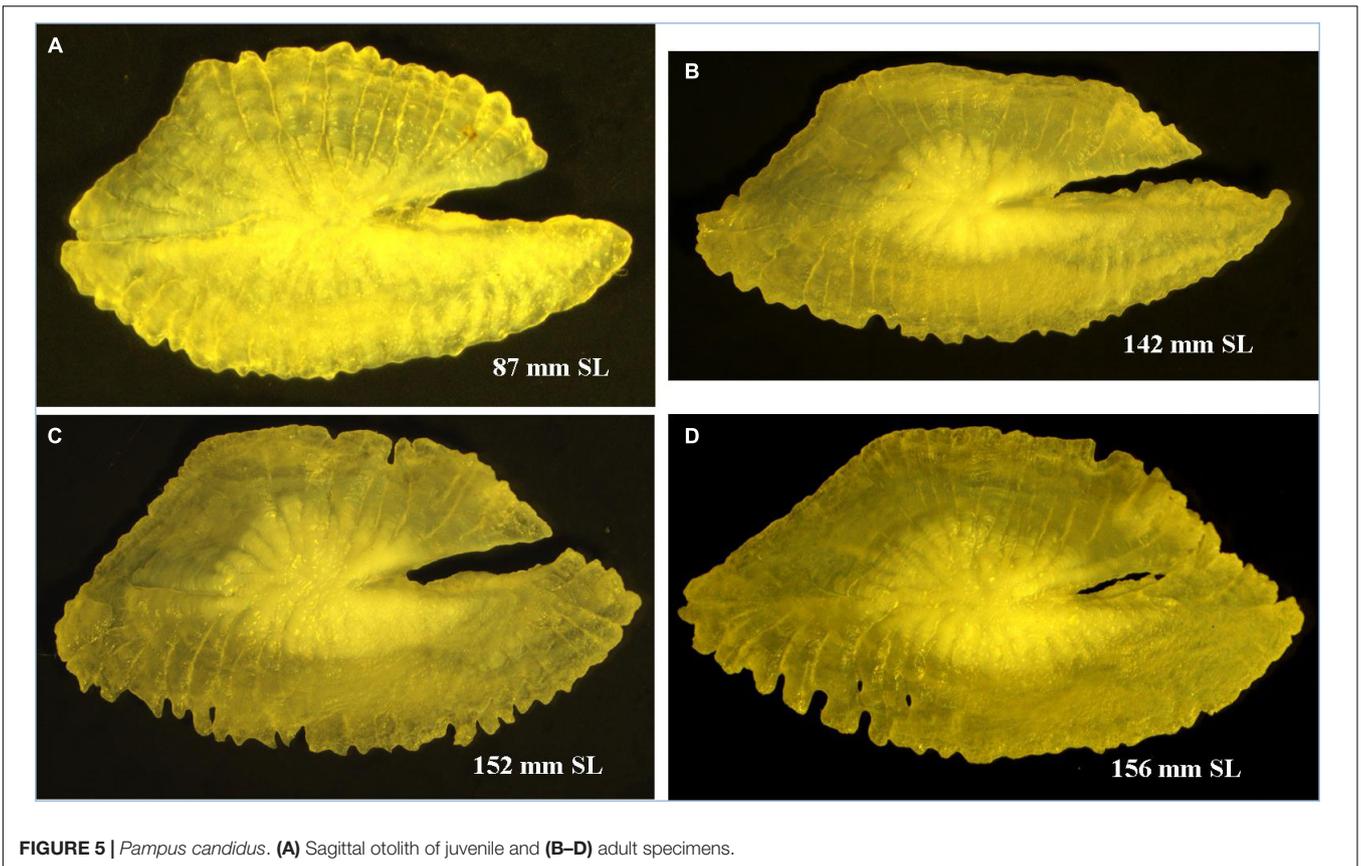


TABLE 3 | Gross description of the sagittal otolith morphology of seven *Pampus* species from the Indo-Western Pacific Oceans based on Zhang et al. (2017) and this study.

Species/Features	<i>Pampus griseus</i>	<i>Pampus cinereus</i>	<i>Pampus candidus</i>	<i>Pampus punctatissimus</i>	<i>Pampus chinensis</i>	<i>Pampus minor</i>	<i>Pampus argenteus</i>
Shape	Oval (smaller) to elliptic (medium) to pentagonal (large), dorsal and ventral margin crenate, crenation uniform in smaller specimens, adults with more pronounced crenation on ventral surface	Pentagonal to elliptic, dorsal and ventral margin crenate	Pentagonal to elliptic, dorsal and ventral margin crenate (more pronounced crenation on ventral margin across all size groups)	Pentagonal to elliptic, dorsal margin crenate, ventral margin dentate to irregular	Pentagonal to elliptic, dorsal and ventral margin crenate (uniform crenation on both surface, becoming less prominent as specimens grows in size)	Oval to elliptic, dorsal and ventral margin crenate to entire	Triangular, dorsal and ventral margin irregular
Sulcus acusticus	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median	Heterosulcoid, ostial, median
Ostium	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda	Funnel-like, shorter than cauda
Cauda	Straight, tubular, terminating near posterior margin	Tubular, straight, ending close to the posterior margin	Straight, tubular, terminating near posterior margin	Tubular, straight, ending close to the posterior margin	Tubular, straight, ending close to posterior margin	Tubular, straight, ending close to posterior margin	Tubular, straight, ending close to posterior margin
Anterior region	Peaked, rostrum long (in large specimen marginally larger than anti-rostrum), broad, pointed; anti-rostrum, short, broad and pointed; excisura wide with deep acute notch (narrow to very narrow in larger specimens)	Peaked, rostrum long, broad, pointed; antirostrum short, broad, pointed; excisura wide with a deep, acute notch	Peaked, rostrum long (in large specimen only marginally larger than anti-rostrum), broad, pointed; anti-rostrum, short, broad and pointed; excisura wide with deep acute notch (narrow to very narrow in larger specimens)	Peaked, rostrum long, broad, pointed; antirostrum short, broad, pointed; excisura wide with a deep, acute notch	Peaked, rostrum long, broad, pointed; antirostrum short, broad, pointed; excisura wide with a deep, acute notch	Peaked, rostrum short, broad, pointed; antirostrum absent; excisura absent	Peaked, rostrum long, broad, pointed; antirostrum short, narrow, pointed; excisura narrow with a shallow notch
Posterior region	Round to oblique	Oblique	Round to oblique	Oblique	Angled	Round	Irregular to oblique

The shape, crenulation, rostrum, excisura, and ventral margin show a pattern in progression from juveniles to adults and, hence, can be used with caution in differentiating and describing the species solely based on otolith morphology.

TABLE 4 | Comparison of the morphological characteristics of seven species of *Pampus* from the Indo-Western Pacific Oceans.

Species/Features	<i>Pampus griseus</i>	<i>Pampus cinereus</i>	<i>Pampus candidus</i>	<i>Pampus punctatissimus</i>	<i>Pampus chinensis</i>	<i>Pampus minor</i>	<i>Pampus argenteus</i>
Overall body shape	Oval	Oval	Oval	Oval	Diamond	Oval	Oval
Body depth	Shorter than standard length minus head	Shorter than standard length minus head	Shorter than standard length minus head	Shorter than standard length minus head	Equal to standard length minus head	Shorter than standard length minus head	Shorter than standard length minus head
Forehead	Not straight	Not straight	Not straight	Not straight	Straight	Not straight	Not straight
Caudal peduncle	Long	Long	Long	Long	Short	Long	Long
Spines preceding median fins	Yes	Yes	Yes	Yes	No	Yes	Yes
Jaw teeth	No branched cusps	No branched cusps	No branched cusps	No branched cusps	Some jaw teeth with three cusps	No branched cusps	No branched cusps
Gill raker shape	Short and rounded	Short and rounded	Short and rounded	Slender and needle-like	Slender and needle-like	Slender and needle-like	Slender and needle-like
Total gill rakers	8–11	7–12	8–12	10–13	10–14	11–16	15–20
Groove on lower ridge of gill cover	Absent	Absent	Absent	Absent	Absent	Absent	Present
Transverse occipital canals of ventral branches of lateral line	Wide, eyebrow-like, slightly longer than dorsal branches, not reaching base of dorsal fin and 1/2 of pectoral fin	Wide, eyebrow-like, almost equal in dorsal branches, not reaching base of dorsal fin and less than 1/2 of pectoral fin	Wide, eyebrow-like, slightly longer than dorsal branches, and not reaching base of dorsal fin, 1/2 of pectoral fin	Slender, eyebrow-like, and longer than dorsal branches, reaching base of dorsal fin and 2/3 of pectoral fin	Slender, eyebrow-like, longer than dorsal branches, reaching base of dorsal fin and 2/3 of pectoral fin	Sparse, eyebrow-like, almost equal or slightly longer than dorsal branches, not reaching base of dorsal fin and 1/2 of pectoral fin	Sparse and shorter than dorsal branches
Total vertebrae	35–36 (rarely 35)	36–38	36–38 (mostly 37–38)	33–37	32–33	29–31	38–42
Eye	Small, diameter less than 1/2 of head length	Small, diameter less than 1/2 of head length	Small, diameter less than 1/2 of head length	Small, diameter less than 1/2 of head length	Small, diameter less than 1/2 of head length	Large, diameter more than 1/2 of head length	Small, diameter less than 1/2 of head length
Pectoral fin	Long	Long	Long	Short	Short	Long	Long
Anal fin	Greatly extended, crossing beyond caudal peduncle	Greatly extended, crossing beyond caudal peduncle	Greatly extended, crossing beyond caudal peduncle	Greatly extended, crossing beyond caudal peduncle	Not extended, never crossing beyond caudal peduncle	Not extended, never crossing beyond caudal peduncle	Not extended, never crossing beyond caudal peduncle
Lower-lobe caudal fin	Greatly extended, almost double than upper in all size classes	Slight extended	Greatly extended, almost double than upper in all size classes	Slight extended	Never extended	Greatly extended almost double than upper in juvenile but nearly equal in adults	Slight extended

by Liu and Li (2013) from Zhuhai fish market, China, re-validated by Jawad and Jig (2017), was recently synonymized with *P. cinereus* (Yin et al., 2019). The molecular analysis in this study could effectively delineate the three species of the *P. cinereus* complex mentioned in Table 1 of Yin et al. (2019) as *P. griseus* (collection from Bangladesh, voucher nos CL1315-2, CL1317, CL1318-1, CL1316-2, CL1320-1, CL1320-2, CL2010, and CL2009), *P. candidus* (collection of uncertain origin, voucher nos CL1975-1, CL1943-1, CL1975-2, CL1975-3, CL2012, and CL1943-2), and *P. cinereus* (South and East China Seas; voucher nos CL1286-3, CL1303-1, and CL1287-2). The genetically close species *P. cinereus*, *P. argenteus*, and *Pampus* sp. identified by Li et al. (2019c) were validated as *P. cinereus*, *P. candidus*, and *Pampus* sp. respectively, the last of which is re-described as *Pampus griseus* (new combination) in this communication. We propose that “*Pampus cinereus* species complex” consists of *P. griseus*, *P. candidus*, and *P. cinereus*, and that this complex is characterized by oval body, long pectoral fin, greatly extended anal fin, slightly to greatly extended lower-lobe of caudal fin, 7–12 short and tubercular-like spinules gill rakers, absence of groove on lower ridge of gill cover, transverse occipital canals of ventral branches of lateral line equal to or slightly longer than dorsal branches, and 36–38 total vertebrae (see Table 4).

Resurrection and Re-description of *Pampus griseus*

New proposed English name: Bengal silver pomfret (Tables 1, 3, 4, Figures 4, 7, and Supplementary Figures 7–11).

Stromateus griseus Cuvier and Valenciennes, 1833: 391 (Pondichéry, Tamil Nadu, India).

Material Examined From India ($n = 35$)

Four ex., 83–110 mm SL, Digha (21°36'58.3272''N, 87°29'56.8644''E), West Bengal, shore seine, 3.5 m, sandy silt, September 12, 2020; 7 ex., 70.6–120.5 mm SL, Puri north landing center (19°47'43.062''N, 85°49'38.5788''E), Puri, Odisha, shore seine, 3–5 m, sandy silt, Aug. 18, 2019; 6 ex., 132–167 mm SL, Paradeep fishing harbor (20°17.345'N, 86°42.422'E), Jagatsingpur, Odisha, trawl, 40–70 m, sandy silt, January 24, 2020; 9 ex., 117–177 mm SL, Atharabanki landing center (20°17'28.2264''N, 86°39'18.738''E), Jagatsingpur, Odisha, India, gillnet, 30 m, sandy silt, June 9 and October 3, 2020; 4 ex., 102–115 mm SL, Visakhapatnam Fishing Harbor (17.696°N, 83.301°E), Andhra Pradesh, trawl, 35–40 m, sandy silt, September 2, 2020; 2 ex., 150–170 mm SL, Puducherry (Pondicherry) fishing harbor (16°3'17.964''N, 78°14'47.49''E), trawl, sandy, Tamil Nadu, October 10, 2020; 3 ex., 150–170 mm SL, Cuddalore Harbor (11°42'52''N, 79°46'31''E), Tamil Nadu, Multiday trawl, 15 m, sandy, October 2020.

Museum Specimens Identified as *Pampus griseus* (Cuvier, in Cuvier and Valenciennes, 1833)

Lectotype (Present Designation)

MNHN-IC-A-5479, 157 mm SL (stuffed), Pondichéry, Tamil Nadu, India (Supplementary Figure 1A); GB.31.145.1.1, 157.2 mm SL, Visakhapatnam, Andhra Pradesh, India, 5–110

m, January 2005, labeled as *P. argenteus* (Supplementary Figure 1C); GB. 31.145.1.8, 136.1 mm SL, West Bengal, India, 60 m, July 24, 2015, labeled as *P. griseus* (Supplementary Figure 1D).

Diagnosis

A species of *Pampus* with the following combination of characters: oval-shaped body, dorsal fin rays VIII–IX 38–42, anal fin rays V–VII 36–39, dorsal fin produced into distinct falcate lobe and anterior lobe of anal fin greatly extended crossing beyond caudal peduncle (54.9–103.2% of SL), preceded by 5–9 small blade-like spines embedded in skin and not prominent in larger specimens (adults); long pectoral fin, 35.1–49.6% of SL; deeply forked caudal fin, lower lobe larger than the upper and greatly extended almost double in all size classes (62–132% of SL); short and tubercular-like spinules gill rakers, 1–2 + 7–9 (8–11); absent groove on the lower ridge of gill cover; ventral transverse occipital canals of lateral line wide, eyebrow-like, slightly longer than dorsal branches, not reaching base of dorsal fin and almost $\frac{1}{2}$ of pectoral fin; sagittal otolith pentagonal to elliptical with uniform crenulation along both dorsal and ventral margin; 35–36 total vertebrae (rarely 35), such as 13–15 precaudal and 21–23 caudal vertebrae.

Description

Counts and proportional measurements of specimens of *P. griseus* are given as percentage of SL in Table 1. D: VIII–IX 38–42; A: V–VII 36–39; P: 22–26; C: 22–26; Gr: 1–2 + 7–9 (8–11); vertebrae 13–15 + 21–23 = 35–36 (rarely 35). Body deep, compressed and oval shape, shorter than the standard length minus head, covered with very small and deciduous cycloid scales; head compressed, dorsal profile strongly keeled, being more prominent behind the eye; small eye its diameter lesser than head length; small mouth, terminal; mouth slit curved downward posteriorly, reaching the middle of the eye; upper jaw not movable, covered with skin; minute teeth on the jaws, in a single row narrowed from the sides without branched cusps; teeth absent on the vomer and palatine; presence of papillae in both halves of pharyngeal sacs; branchiostegal membrane fused with isthmus; gill membranes joined to belly, gill slit longer, its lower margin below the level of pectoral-fin base; short and tubercular-like spinules gill rakers with 8–11 (total) on first first-gill arch (Supplementary Figure 8); both dorsal and anal fin lobe-like anteriorly, preceded by 8–9 and 5–7 small, blade-like spines, embedded in skin in larger specimens, respectively; anterior rays (lobe) of anal fin always greatly extended, crossing beyond the caudal peduncle in all size classes (Figure 7); long pectoral fins; almost equal dorsal and anal fin base lengths; deeply forked caudal fin, lower lobe larger than the upper and always greatly extended in all size classes, almost double than upper lobe (Figure 7); absence of groove on the lower ridge of gill cover (Supplementary Figure 9); transverse occipital canals and dorsal branches of the lateral-line canal on top of the head with a truncated rear edge; wide ventral branches, eyebrow-like and slightly longer than the upper branches, not reaching the origin of the dorsal fin, and nearly $\frac{1}{2}$ of the pectoral fin length (Supplementary Figure 10); lateral line is high, following dorsal profile to caudal peduncle.

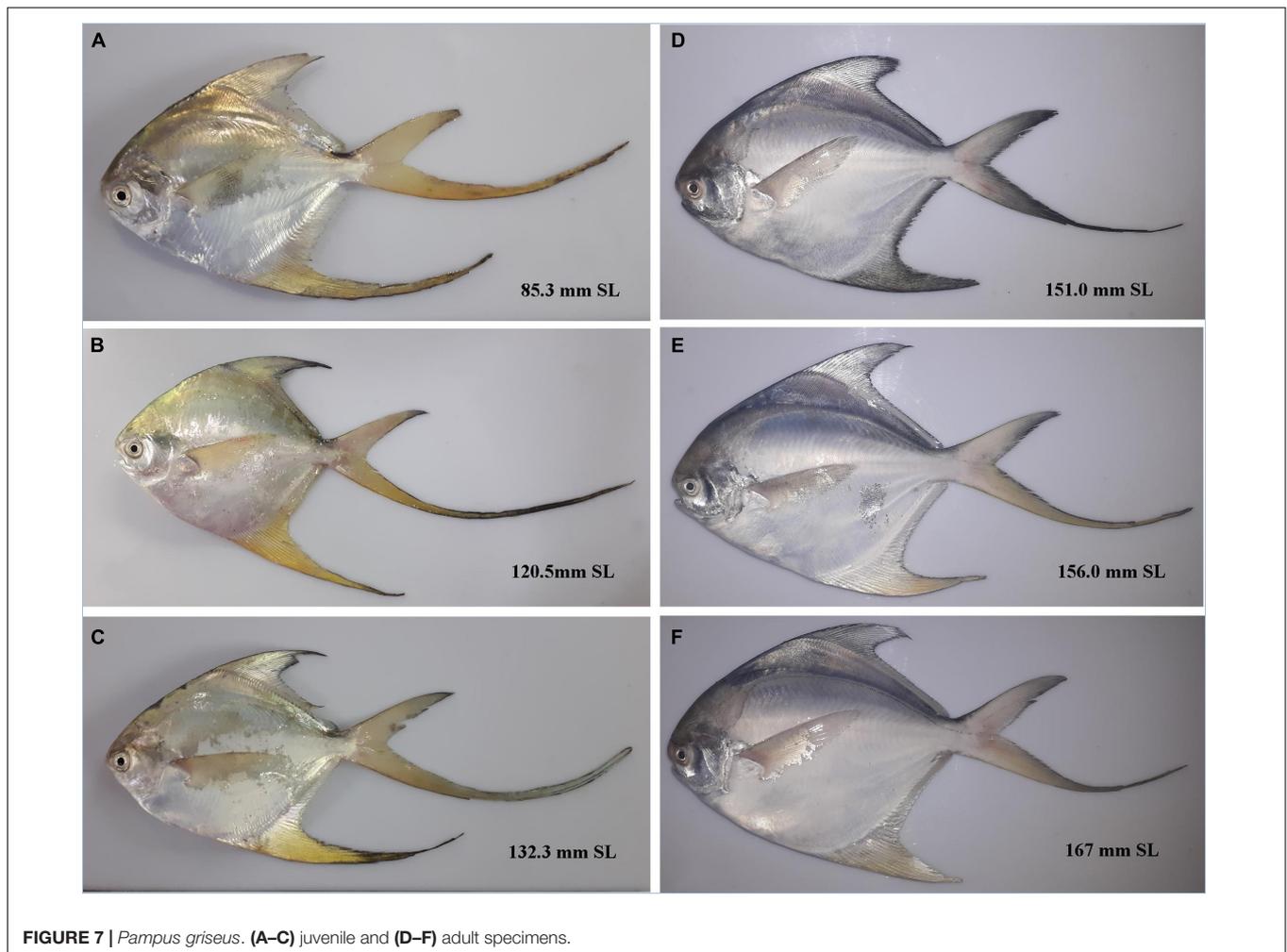


FIGURE 7 | *Pampus griseus*. (A–C) juvenile and (D–F) adult specimens.

Sagittal Otolith Morphology

The sagittal otolith of *P. griseus* showed a marginal transformation in its shape with an increase in size of the fish (61–151 mm SL). The major transformation was evident in depth (dorsal-ventral axis) to length (anterior-posterior axis) ratio, which was found smaller in the case of otoliths of larger specimens (Figure 4). The otolith, in general, can be characterized by a pentagonal to elliptical shape with uniform crenulation along both the dorsal and ventral margins (Supplementary Figure 7). The depth of incision in crenulation tends to decrease as the size of the otolith increases. The heterosulcoid otolith with funnel-shaped ostia is shorter than the tubular and straight cauda. The rostrum is long and pointed in contrast to anti-rostrum, which is shorter but pointed. The excisura major was deep with acute oblique notch (Table 3).

Habitat

Inhabits inshore shallow waters of various bottom types: sandy silt, rocky, and turbid muddy bottoms; usually moves in large schools; juveniles found in the depth gradient of 3–30 m, whereas subadults and adults mostly at 30–70 m. Specimens were observed and obtained from various locations along the east coast of India (Bay of Bengal) from different fishing gears: ring seines

(bunt mesh size 10 mm, wing and shoulder mesh size 15 mm) affirmed at 12–18 m water depth; shore seines (bag mesh size 5–10 mm, wing mesh size 15–20 mm) operated at 3–5 m water depth; trawls (cod-end mesh size 40 mm) operated at 30–100 m water depth; and gill nets (mesh size 45–58 mm) operated at 10–30 m water depth.

Color of Live Specimens (Supplementary Figure 12)

Color description is based on the live specimens observed in the ring seines and shore seines. The dorsal and lateral surfaces of head and body above pectoral fin aquamarine blue; silvery on ventral side below pectoral fin area; dorsal fin grayish silvery with blackish outer margin; anal fin light to dark yellowish with blackish outer margins; pectoral fin translucent and light yellowish or hyaline; caudal fin light yellowish with blackish outer margin and silver-blue tinge toward the tip of both lobes; minute black dots covered almost entire the body, which generally got removed or disappeared during fishing and post-harvest handling; faint blackish spot on the upper part of the opercle; some specimens, mostly young ones, are much darker than the adults, and all the fins nearly blackish or grayish in appearance.

Color of Formalin-Preserved Specimens

Dorsal and lateral surfaces of the body and head brownish tan, fading to pale creamy or brownish toward ventral sides. All fins are yellowish-brown toward the base with dusky margin posteriorly.

Geographic Distribution

This study and the GenBank records (COI, Cyt *b*, ATP6/8, and 16s rRNA sequences) suggest that *P. griseus* has a restricted distribution in the Bay of Bengal (East coast of India, Bangladesh, Myanmar) and Southeast Asia (Thailand, Vietnam, and Malaysia) (Supplementary Tables 2–4 and Supplementary Figure 2).

Etymology

The species was named “griseus” in the original description with reference to the gray color of the body. The new English name “Bengal silver pomfret” is proposed for this species since its type locality falls in the Bay of Bengal and it forms the major component in pomfret fishery of the region.

Pampus candidus (Cuvier, in Cuvier and Valenciennes, 1833)

New proposed English name: Indian silver pomfret (Tables 1, 3, 4, Figures 5, 8, and Supplementary Figures 7–11).

Pampus candidus was recently resurrected from the synonymy with *P. argenteus* and re-described as a valid species by Divya et al. (2019) based on fresh specimens from the Arabian Sea and the Bay of Bengal, and a lectotype was designated in the absence of type specimen. Their study provided the count D. VII–IX 40–42, A. V–VII 36–41, P. 22–24, C. 22–24, Gr. 1–2 + 6–8 = 8–10, and vertebrae 16 + 21 = 37. Similar counts with some variation were observed by Li et al. (2019c) where they misidentified *P. candidus* to *P. argenteus* (validated in this study); with counts concurrent to this study, i.e., D., D. VII–X, 36–42, A. V–VI, 36–40, P. 22–28, C. 22–28, Gr. 1–2 + 7–9 = 9–11 and vertebrae 36–38 (mostly 37–38, rarely 36) such as 14 precaudal and 22–24 caudal vertebrae. Divya et al. (2019) had stated the presence of extended lower lobe of caudal fin in subadults that progressively shortens with age to lobes of almost equal length in specimens over 100 mm SL, contrary to the observation of this study, wherein the extended lower lobe for caudal fin could be observed in all size groups (see Figure 8). It may be summarized that *P. candidus* is distributed in the Persian Gulf (Iran, Iraq, and Kuwait), Oman Sea, Arabian Sea (Pakistan and west coast of India), Bay of Bengal (West Bengal and Tamil Nadu), China Sea (Xiamen, Taiwan, and Beibu Bay), Southeast Asia (Malaysia and Indonesia), sporadically occurring in the Southern Pacific (Fowler, 1938), Adriatic Sea, North Sea, and the Mediterranean Sea (Dulčić et al., 2004; Piper, 2010; Sami et al., 2014). A new English name “Indian silver pomfret” is also proposed for this species, since it represents the predominant species in the Indian Ocean and is originally described as *Stromateus candidus* Cuvier and Valenciennes (1833) from Indian waters.

Pampus cinereus (Bloch, 1795)

Gray pomfret (Tables 3, 4 and Supplementary Figures 7–11).

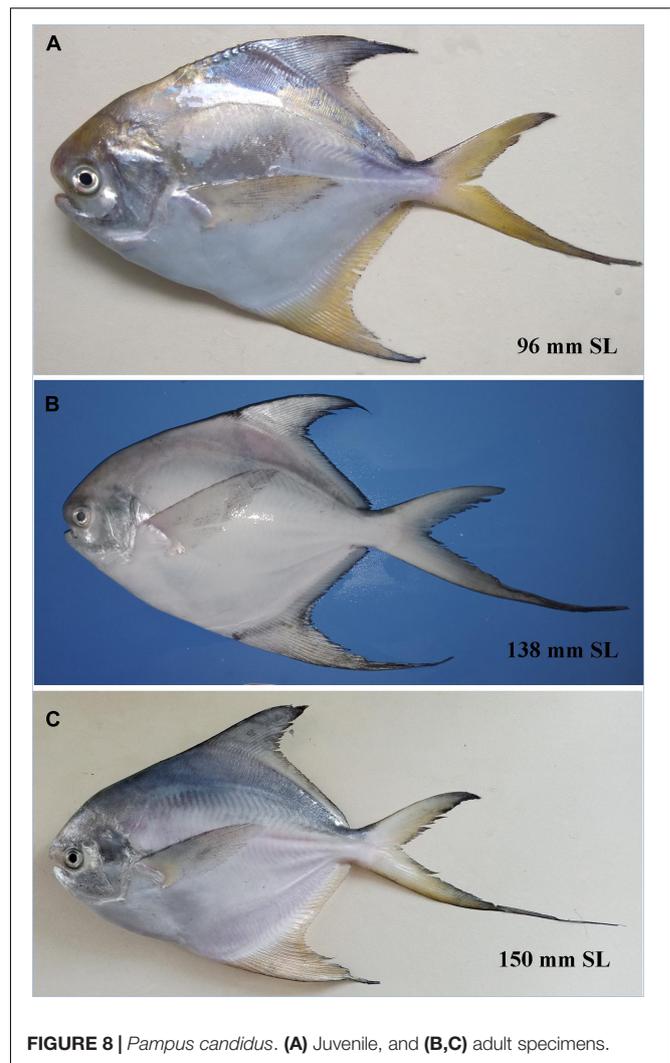


FIGURE 8 | *Pampus candidus*. (A) Juvenile, and (B,C) adult specimens.

Pampus cinereus was believed to be a common species distributed in the Indo-Western Pacific Oceans. The species was originally described by Bloch (1795) as *Stromateus cinereus* based on a single stuffed specimen without any information on type locality, whereas in a later publication, Bloch and Schneider (1801) mentioned it as Tranquebar (Tharangambadi, Tamil Nadu). However, recently, Li et al. (2019c) mentioned Malaysia as the type locality for the species. The only diagnostic characteristics provided in the original description of the species are greatly extended anal fin and distinctly long pectoral fins. In subsequent publications, *P. cinereus* was considered as a synonym of *P. argenteus* (Haedrich, 1967; Lindberg and Krasnyukova, 1975; Parin and Piotrovsky, 2004; Li et al. 2013, 2017; Sun, 2015), but it was later accepted as a valid species through morphological (Regan, 1902; Wu, 1985; Cui et al., 2010, 2011; Liu et al., 2013a; Jawad and Jig, 2017; Zhang et al., 2017) and molecular studies (Divya et al., 2017, 2019; Li et al., 2019c; Yin et al., 2019). Due to insufficient information in Bloch's original description and loss of the original type specimen, Liu et al. (2013a) re-described *P. cinereus* based on fresh specimens from Guangdong, South

China Sea, and a neotype was designated. Their study provides the counts of D. VIII–X 37–41, A. V–VII 36–41, P. 20–22, C. 22–24, Gr. 1–2 + 6–8 = 7–10 and vertebrae 15 + 21 = 36. Later, Jawad and Jig (2017) confirmed the identity of *P. cinereus* based on osteology where they counted vertebrae. Zhang et al. (2017) also retained the species status of *P. cinereus* based on sagittal otolith morphology. Li et al. (2019c) provided the vertebrae counts (37–38) with some variations from Liu et al. (2013a). Yin et al. (2019) recorded 36–37 vertebrae for *P. cinereus* and 36–38 for *P. liuorum*, and considered the latter to be a synonym. However, their vertebral count of *P. cinereus* could be ambiguous, since they considered the three species (*P. candidus*, *P. griseus*, and *P. cinereus*) as complex. Based on the available data in GenBank, and the recent studies (Li et al., 2019c; Yin et al., 2019), we concluded that *P. cinereus* is completely absent in India and distributed in the western Pacific Ocean throughout the waters south of Taiwan Strait and those extending southward toward the Malaysian peninsula (Supplementary Table 3).

***Pampus chinensis* (Euphrasen, 1788)**

Chinese silver pomfret (Tables 1, 3, 4, Figures 6, 9, and Supplementary Figures 7–11).

Pampus chinensis is a commercially important species, widely distributed in the Indo-Western Pacific Oceans. The species was originally described as *Stromateus chinensis* by Euphrasen (1788) from “Castellum Chinese Bocca Tigris,” Humen, Guangdong province, China. Since then, the species has been renamed and described in various names: *Stromateus sinensis* (Forster, 1795), *S. atous*, and *S. albus* (Cuvier and Valenciennes, 1833), *Stromateoides atous* (Richardson, 1846), *S. atokoia* (Bleeker, 1851), *S. atoukoia* (Bleeker, 1852), *S. sinensis* (Regan, 1902), and *Pampus chinensis* (Beaufort and Chapman, 1951; Haedrich, 1967). Currently, all the names are considered as synonyms of the accepted *P. chinensis*. The diagnostic characteristics, such as vertebral count 33; no spines preceding the median fins; fins never deeply falcate and the fin rays gradually and uniformly diminishing in length posteriorly, were provided in the Euphrasen’s original description of *P. chinensis*. Recently, several authors have also affirmed the identity of the species based on morphological examination and molecular analyses. Li et al. (2019c) provided the counts D. V–VI 41–46, A. IV–VI 40–41, P. 20–22, C. 22–24, Gr. 2–3 + 9–10 = 11–13 and vertebrae 32–33. However, their dorsal and anal fin ray counts were erroneous, and they seem to include separately some anterior smaller rays as spine, which is completely absent in *P. chinensis*. Our study counted D. 41–49, A. 38–45, P. 20–27, C. 18–28, Gr. 1–4 + 8–11 = 9–14 and total vertebrae 32–33 (rarely 32), such as 12–14 precaudal and 19–21 caudal vertebrae. Overlapping counts for vertebrae were provided by Jawad and Jig (2017) and Yin et al. (2019). Comparative COI (Divya et al., 2017; Li et al., 2019c) and multiple marker-based studies indicated that *P. chinensis* from the Indian Ocean (Arabian Sea) formed a distinct lineage from the Pacific (Li et al., 2019a), and a detailed study covering entire areas of species distribution is recommended. The Chinese silver pomfret population, distributed along India, does not differ significantly from that in the Pacific in morphology or other features covered in this study. The overall analysis led to the

assumption that the species is mainly distributed in the Arabian Sea, the Bay of Bengal, and in waters south of the East China Sea, South China Sea, and that it may also be distributed throughout the coastal areas of Southeast Asian countries, such as Malaysia (Liu et al., 2002; Yamada et al., 2009; Divya et al., 2017; Li et al., 2019a,c; Yin et al., 2019; present study).

***Pampus punctatissimus* (Temminck and Schlegel, 1845)**

New proposed English name: Japanese silver pomfret (Tables 3, 4 and Supplementary Figures 7–11).

Pampus punctatissimus is an economically important species, widely distributed in the Western Pacific. The species was originally described as *Stromateus punctatissimus* by Temminck and Schlegel (1845) based on two specimens (whose fins were damaged) from Nagasaki, Japan. Later, the species was synonymized with *P. argenteus* by some authors (Bleeker, 1852; Haedrich, 1967) because of their morphological similarities. The original description lacks some of the important diagnostic characteristics, such as gill raker and vertebra count; hence, Liu and Li (1998b) re-described *P. punctatissimus* in detail based on specimens collected from Chinese coastal waters and compared its morphology with that of *P. argenteus* to resolve the taxonomic ambiguity of the species. In subsequent publications, the identity of the species was confirmed based on detailed osteology, sagittal otolith morphology, and integrative taxonomy (Dolganov et al., 2007; Jawad and Jig, 2017; Zhang et al., 2017; Li et al., 2019c; Yin et al., 2019). Li et al. (2019c) gave counts D. V–VII 39–48, A. V–VII 32–42, P. 22–25, C. 23–26, Gr. 2–3 + 9–10 = 11–13, and vertebrae 33–35 for *P. punctatissimus*. Overlapping counts for vertebrae were provided by several authors: 34–37 (Dolganov et al., 2007), 34 (Jawad and Jig, 2017), and 35 (Yin et al., 2019). The available information suggests that *P. punctatissimus* is distributed in the western Pacific Ocean, namely, the Sea of Japan, Pacific coast of Japan, Korean Peninsula, Yellow Sea, the East China Sea, and South China Sea, and that its distribution might even extend southward toward the Indonesian Islands. A new English name “Japanese silver pomfret” is proposed for this species in commemoration of its original description from the Japanese waters.

***Pampus argenteus* (Euphrasen, 1788)**

Silver pomfret (Tables 3, 4 and Supplementary Figures 7–11).

Pampus argenteus was believed to be the most widely distributed *Pampus* in the Indo-Western Pacific and the most commercially important of all, remained the most controversial until recent past. The species was first described as *Stromateoides argenteus* by Euphrasen (1788) based on a single specimen from “Castellum Chinese Bocca Tigris,” Guangdong province, China. Most species of *Pampus* were considered to be synonyms of *P. argenteus* for several years before they were described, re-described, and resurrected (Liu and Li, 1998a,b; Liu et al., 2013a,b; Divya et al., 2019; This study). Because of difficulty in locating the type specimen and ambiguity in Euphrasen’s original description, Liu et al. (2013b) re-described *P. argenteus* based on the specimens collected from the type locality, and a neotype was

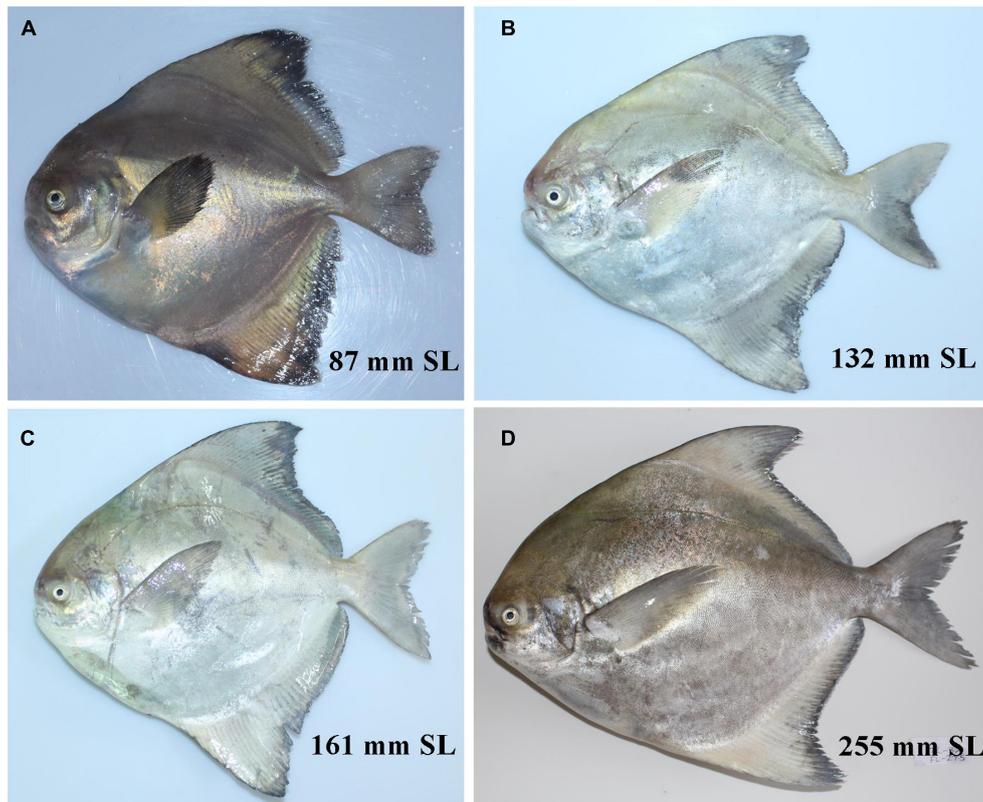


FIGURE 9 | *Pampus chinensis*. (A) Juvenile, (B,C) subadult, and (D) adult specimens.

designated. Another species, *Pampus echinogaster*, was described as *Stromateoides echinogaster* by Basilewsky (1855) from the Gulf of Chihli (Bohai), Beijing, China. Later, the validity of the species was ascertained by several authors (Haedrich, 1967; Jawad and Jig, 2017; Li et al., 2017, 2019c). The original description of *P. echinogaster* did not include meristics, and modern ichthyologists could not locate its type specimen. Therefore, Li et al. (2017) re-described *P. echinogaster* and validated the identity of the species based on specimens collected from China and Japan, and was again confirmed by Li et al. (2019c). However, during the same year, Yin et al. (2019), through an extensive study, established that *P. echinogaster* is not a valid species but a synonym of *P. argenteus* based on examinations of specimens from the South China Sea, type locality of *P. argenteus* and the Bohai Sea, and type locality of *P. echinogaster*. Their study concluded that Euphrasen's original morphologic description of *P. argenteus* and *P. echinogaster*, described by Haedrich (1967), is *P. argenteus* according to the number of its fin rays and gill raker count, but that Haedrich's *P. argenteus* is potentially another species. In re-description of *P. argenteus*, Liu et al. (2013a) provided overlapping counts with *P. echinogaster* and distinguished both the species mainly based on vertebral count (40 vs 40–41). Jawad and Jig (2017) reported the vertebral count, *P. echinogaster* (39) vs. *P. argenteus* (41), whereas Yin et al. (2019) gave the vertebral count, 41 vs 39–40. The above-mentioned studies support that the two species should be treated as same as "*P. argenteus*." The current knowledge affirms

that *P. argenteus* is completely absent in the Indian Ocean and is primarily distributed in the Western Pacific: Pacific coast of Japan, Sea of Japan (East Sea), Korean Peninsula, South China Sea, East China Sea, Bohai Sea, and Yellow Sea.

***Pampus minor* Liu and Li, 1998**

Southern lesser pomfret (Tables 3, 4 and Supplementary Figures 7–11).

Pampus minor is a small-sized pomfret widely distributed in the Western Pacific. The species was originally described by Liu and Li (1998a) based on 32 specimens from the coastal waters of the South China Sea and the continental coast of the Taiwan Strait. Because of the smaller size of adult fish, *P. minor* was previously mistaken as the juvenile or larvae of *P. argenteus* and *P. cinereus* (Liu and Li, 1998a). Later on, the species was confirmed based on morphological and molecular data (Guo et al., 2010; Jawad and Jig, 2017; Zhang et al., 2017; Li et al., 2019c; Yin et al., 2019; Liu et al., 2020). Li et al. (2019c) and Liu et al. (2020) provided the counts D. VII–IX 34–39, A. V–VII 35–39, P. 22–24, C. 18–20; Gr. 3–4 + 8–10 = 11–14; and vertebrae 29–31 with some variations in gill raker and vertebra counts in comparison with the original description. Overlapping vertebra counts were provided by Jawad and Jig (2017), 30, and Yin et al. (2019), 29, for *P. minor*. Based on the literature (Li et al., 2019b,c; Yin et al., 2019; Liu et al., 2020), we confirmed that *P. minor* is mainly distributed in the southern part of the Taiwan Strait and the northern part

of the South China Sea and Beibu Gulf, with its northernmost distribution reaching the coastal waters of Wenzhou, China (East China Sea) and coastal areas of Southeast Asian countries, such as Malaysian waters.

Key to Species Identification

For morphological synapomorphies, identification of species in *Pampus* is at times difficult. Yin et al. (2019) developed a convenient identification key for five species, whereas Li et al. (2019c) provided a key for six species, such as *P. echinogaster*, from the Western Pacific. However, both the keys are incomplete, as they lack representation of *P. candidus* and *P. griseus*, which form the major fishery in the Indian subcontinent, and correctly identifying them is important. The seven species of pomfrets (*P. griseus*, *P. candidus*, *P. cinereus*, *P. chinensis*, *P. punctatissimus*, *P. argenteus*, and *P. minor*) discussed in this study can be distinguished based on the diagnostic characteristics given in Table 4. A simple key for all the known congeners adapted from Li et al. (2019c); Yin et al. (2019), and this study is provided below.

- 1a Body has a diamond shape, very deep equal to standard length minus head length, forehead almost straight, short caudal peduncle, some jaw teeth having three cusps, caudal fin deeply forked and both upper and lower lobes equal in length, anal fin and caudal fin not extended, and no spines preceding the median fins.....*P. chinensis* (Euphrasen, 1788).
- 1b Body has an oval shape, body depth smaller than standard length minus head length, forehead not straight, long caudal peduncle, jaw teeth without branched cusps, caudal fin deeply forked and lower lobe larger than the upper, anal fin and caudal fin slight to greatly extended, and spines preceding the median fins..... 2
- 2a Gill rakers short and tubercular-like spinules..... 3
- 2b Gill rakers slender and needle-like..... 5
- 3a Transverse occipital canals of the ventral branches of lateral line almost equal to the dorsal branches and less than 1/2 of pectoral fin length; caudal fin lower lobe slight extended..... *P. cinereus* (Bloch, 1795).
- 3b Transverse occipital canals of the ventral branches of lateral line longer than dorsal branches, not reaching base of dorsal fin and 1/2 of pectoral fin; caudal fin lower lobe greatly extended..... 4
- 4a Total vertebrae, 36–38 (mostly 37–38)..... *P. candidus* (Cuvier, in Cuvier and Valenciennes, 1833).
- 4b Total vertebrae, 35–36 (rarely 35).....*P. griseus* (Cuvier, in Cuvier and Valenciennes, 1833).
- 5a Groove present on the lower ridge of gill cover, gill rakers 15–20, vertebrae 38–42, transverse occipital canals of ventral branches of lateral line sparse and shorter than dorsal branches.....*P. argenteus* (Euphrasen, 1788).
- 5b Groove absent on the lower ridge of gill cover; gill rakers 10–16, vertebrae 29–37, transverse occipital canals of

ventral branches of lateral line equal or longer than dorsal branches..... 6

- 6a Transverse occipital canals of the ventral branches of lateral line longer than dorsal branches, reaching base of dorsal fin and 2/3 of pectoral fin; vertebrae: 33–37; pectoral fin short; eye small, diameter less than 1/2 of head length.....*P. punctatissimus* (Temminck and Schlegel, 1845).
- 6b Transverse occipital canals of the ventral branches of lateral line almost equal or slightly longer than dorsal branches, not reaching base of dorsal fin and 1/2 of pectoral fin; vertebrae: 29–31; pectoral fin long; eye large, diameter more than 1/2 of head length.....*P. minor* (Liu and Li, 1998).

Taxonomic Archives of Indian Stromateids

The taxonomy of pomfrets (*Pampus*) in Indian waters dates back to 1803 when Russell described four species under the *Stromateus* genus from Visakhapatnam (Visagapatnam) on the Coromandel Coast of India (Russell, 1803): *Stromateus argenteus* (*Stromateus* with squamous rhomboidal body, Tella Sandawa); *S. niger* (*Stromateus* with squamous ovate body, Nala Sandawah); *Stromateus* with body nearly orbicular, covered with small scales (Atooo Koia); and *Stromateus* with rhombiform body, without scales (Sudi Sandawah). Subsequently, five species of stromateids were described in Cuvier and Valenciennes (1833): *S. candidus*, *S. securifer*, *S. griseus*, *S. albus*, and *S. atous*. Day (1876) recorded three species of pomfrets (*S. cinereus*, *S. sinensis*, and *S. niger*) from the Indian seas. Of the species of *Stromateus* mentioned above, Russell's Atooo Koia (a species similar to *Pampus chinensis*) and Sudi Sandawah (based on description of an immature specimen) are native names and, thus, were not used by subsequent authors [see Plate-XLIV and Plate-V in Russell (1803)]. Haedrich (1967) synonymized the four species, *S. candidus*, *S. griseus*, *S. securifer*, and *S. cinereus*, to *Pampus argenteus* and two species, *S. albus* and *S. atous*, described from Indian waters to *P. chinensis*. However, recently, many species of *Pampus* were resurrected and re-described, like *P. cinereus* (Liu et al., 2013a) and *P. candidus* (Divya et al., 2019). While examining the *Pampus* species from India, our study revealed that the specimens from the east coast (West Bengal, Odisha, Andhra Pradesh and Tamil Nadu) in the Bay of Bengal are sufficiently distinct from the closely related congener *P. candidus* from India and *P. cinereus* from the South China Sea both at morphological and molecular levels.

Pampus griseus is originally described as *Stromateus griseus* by Cuvier and Valenciennes (1833), with counts D. 7–1/40, A. 5–1/38, C. 28, P.23 and caudal fin divided into two acute lobes, lower one nearly double in length than the upper, matches well with Russell's Sudi Sandawah [see descriptions and Plate-XLV in Russell (1803)], the second valid species in this study (Table 1 and Figure 7). The type locality of

both *S. candidus* and *S. griseus* was mentioned as Puducherry in the original description; therefore, the authors revisited, collected, and examined several specimens from the type locality (Puducherry) and nearby areas, such as Rameshwaram (Palk Bay), Nagapattinam, and Cuddalore, along the coast of Tamil Nadu in order ascertain the species. All the specimens examined from these areas were confirmed and identified to be either *P. candidus* or *P. griseus*. Also, there exist GenBank records of *P. candidus* from Karaikal (KX530944–KX530948) and Chennai (KF373001–KF373002) by Divya et al. (2017). *S. griseus* is represented by two syntypes (MNHN-IC-A-5479 and MNHN-IC-A-5512) at the Muséum National d'Histoire Naturelle (Fricke et al., 2020). Examination of the digital images of syntypes revealed that both the specimens are under dried and poor conditions, which makes it impossible to extract the correct morpho-meristic measurements to compare with the present fresh materials (source: <https://science.mnhn.fr/institution/mnhn/collection/ic/item/a-5512> and <https://science.mnhn.fr/institution/mnhn/collection/ic/item/a-5479>). MNHN-IC-A-5479 (**Supplementary Figure 1A**) may be probably the specimen of *P. griseus* collected from Pondicherry (Puducherry), Tamil Nadu on the east coast of India, whereas MNHN-IC-A-5512 is obviously a specimen of *Parastromateus niger* (**Supplementary Figure 1B**). Examination of the drawing and description of Sudi Sandawah and Tella Sandawa from Visakhapatnam revealed that Sudi Sandawah is identical to the immature specimens examined in this study in that it has greatly extended anal and caudal fins (**Supplementary Figure 13A**); Tella Sandawa is also identical to the subadult and adult specimens examined in this study in that it has similar morphology of transverse occipital canal but differs because of having short anal and caudal fins (**Supplementary Figure 13B**). Russell's Tella Sandawa might have been drawn from a specimen with broken caudal and lower lobe caudal fins (personal observation). The authors also revisited and examined the specimens from Visakhapatnam (type locality) and nearby areas (Odisha and West Bengal) and confirmed it as the second valid species. Sudi Sandawah is the native name and, thus, cannot be retained as species name, and the Tella Sandawa described as *P. argenteus* may be probably the specimen of the second valid species in the Bay of Bengal. Therefore, we prefer to retain a valid species status by providing the earlier described Indian species as *Stromateus griseus* from Pondicherry resurrecting it from the synonymy of *P. argenteus* and re-described as *Pampus griseus* (Cuvier, in Cuvier and Valenciennes, 1833) in the Bay of Bengal based on an integrative taxonomic approach. A lectotype (MNHN-IC-A-5479) was designated for *Stromateus griseus* to identify the species and fix the name. Additionally, two preserved specimens, GB. 31.145.1.8 (136.1 mm SL), labeled as *P. griseus* from West Bengal (**Supplementary Figure 1D**), and GB.31.145.1.1 (157.2 mm SL), labeled as *P. argenteus* from Visakhapatnam, Andhra Pradesh (**Supplementary Figure 1C**) deposited in the Marine Biodiversity Referral Museum of ICAR-Central Marine Fisheries Research Institute (CMFRI), Cochin, Kerala, India were re-examined and presumed to be *P. griseus*.

Remarks on Phenotypic Similarities and Distribution

In overall body appearance, *P. griseus* is similar to *P. candidus* and *P. cinereus*, which form a closely related complex (**Table 4** and **Supplementary Figure 10**). Anal fin, greatly extended in *P. griseus* and *P. candidus* crossing beyond the caudal peduncle, was observed in this study (**Figures 7, 8**). Conversely, Liu et al. (2013a) provided an opposite character where the extended anal fin reaches behind the caudal peduncle, as reflected in Bloch's original drawings (see Figure 1B in Liu et al., 2013a). However, after a thorough examination of a colored photograph of *P. cinereus* (see Figure 1A in Liu et al., 2013a), it was evident that the tip of the anal fin would have been broken but crossing beyond the caudal peduncle, a feature that was overlooked by Liu et al. (2013a). The long deeply forked caudal fin, with the lower lobe longer than upper and extended almost double in length is a feature in all size classes of *P. griseus* and *P. candidus* (**Figures 7, 8**), which is only slightly extended in *P. cinereus* (see Figure 1A in Liu et al., 2013a). This study refutes the observation of shortening of lower caudal fin lobe with age (Divya et al., 2019), and assumes that this feature may not be considered as an important character to distinguish species. The thin and fragile extended fins in most pomfret species frequently get damaged/cut either during fishing operation and post-harvest handling, or sometimes because of predator attacks (personal observation; Almatar and Chen, 2010), and urges the need for utmost care during taxonomic investigation of specimens, which can easily be overlooked by researchers.

This study that covered the Indian coastline suggested that the three species sympatric in the Indian Ocean vary in range of distribution and abundance; *P. chinensis* has a wider distribution compared to *P. candidus*, which occurs in Arabian Sea and certain areas of the BOB (Rameshwaram, Karaikal, Nagapattinam, and Chennai of Tamil Nadu), while *P. griseus* is distributed exclusively in Cuddalore (Tamil Nadu), Puducherry (type locality), Andhra Pradesh, Odisha, and West Bengal in the BOB. It is interesting to note that although both the species are present in Tamil Nadu (BOB), only *P. griseus* could be traced from the fishing harbors of the type locality and regions adjacent to Cuddalore. This study hinted *P. griseus* as the dominant species in fishing harbors of West Bengal and Andhra Pradesh, as evidenced by the ATPase sequences submitted by Divya et al. (2015). However, the presence of two COI barcodes (KF373009–KF373010; Divya et al., 2017) of *P. candidus* from West Bengal cannot be ignored and hinted at the rare chance of its occurrence in this area.

However, sporadic catches of *Pampus argenteus* beyond its native ranges (Indo-Western Pacific Oceans) such as Adriatic Sea, Southern Pacific, North Sea, and Mediterranean Sea (Fowler, 1938; Dulčić et al., 2004; Piper, 2010; Sami et al., 2014) were reported. Such records, except for the Southern Pacific, may be attributed to the Lessepsian migration of pomfrets through the Suez Canal and then to the Adriatic Sea and the northeastern Atlantic, consistent with the hypothesis that pomfret followed a slow-moving vessel or maintained an association with pelagic medusa (Sami et al., 2014). The morphological similarities of this complex group, coupled with absence of detailed morphological

and molecular data, create ambiguity in establishing the occurrence of true “*P. argenteus*” in the indicated areas. The re-description of *P. candidus* and reported absence of *P. argenteus* from the Indian Ocean (Divya et al., 2019) affirm that *P. argenteus* is endemic to western Pacific Oceans. Thus, the reports from the Adriatic, North, and Mediterranean Seas can probably represent *P. candidus* or potentially another species that needs to be validated.

CONCLUSION

The classification of the genus *Pampus* has long been a subject of research with persistent controversies, and the results have struggled to be consistent and uniform, which imparted little scope to morphological distinction among some taxa. Therefore, classical taxonomy alone may not be suitable to resolve the systematics of the genus. Erroneous submissions in the GenBank database indicated that nominations based only on monogenic barcodes can be jeopardous. An integrative approach coupling DNA-based analysis and traditional taxonomy is the most authentic and informative tool used for delineating novel species and revitalizing taxonomy (Rajpoot et al., 2016). In this study, we have successfully employed this method to effectively resurrect the cryptic and valid species “*Pampus griseus*”. Misidentifications of sequences in the NCBI database were corrected based on reference sequences and recent literature to reconstruct the Bayesian phylogeny of the genus, which resulted in seven clades representing the seven species distributed in the Indo-Pacific, of which three (*P. chinensis*, *P. candidus*, and *P. griseus*) having distribution in the Indian Ocean. We confirmed that *Pampus chinensis* from Indian and Pacific Oceans represent two distinct lineages of single species unlike reported earlier. Major diagnostic characteristics were identified, systematics of genus *Pampus* was reviewed, and an easy field identification key was provided based on a combination of features. A future study on its distributional ranges is obligatory to have detailed information on fishery, biology, and population parameters of this species, which will help fishery managers for sustainable exploitation and proper management.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.ncbi.nlm.nih.gov/>, MW422591–MW422604, MW421904–MW421919, MW343690–MW343704, MW366881–MW366888,

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MW419276–MW419288, MW337238–MW337245, MW343460–MW343467, MW332295–MW332304, MW260616–MW260617, MW343468–MW343475, MW447297, MW447300–MW447301, and MW456736.

AUTHOR CONTRIBUTIONS

SRo and NJ conceptualized the work, analyzed the morphological and molecular data respectively, and wrote the complete manuscript in concurrence. ShR and RK provided specimens, fishery, and export information of *P. candidus* from Gujarat, and described otolith morphology. SuR carried out the molecular lab works. RV sampled from Tamil Nadu (East Coast of India). SG arranged specimens from Visakhapatnam. PR and SG critically reviewed and corrected the write up. AG co-ordinated the work. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.778422/full#supplementary-material>

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