

## RESEARCH ARTICLE OPEN ACCESS

# Ending the Decades-Long Debate: *Trachinotus anak* Ogilby, 1909 is the Correct Scientific Name of Golden Pompano in Chinese Aquaculture

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**Received:** 24 October 2025 | **Revised:** 23 December 2025 | **Accepted:** 5 February 2026

**Academic Editor:** Kar Hoe Loh

**Keywords:** correct scientific name | golden pompano | mariculture | *Trachinotus ovatus* | *Trachinotus anak*

## ABSTRACT

The debate over the correct scientific name of golden pompano in Chinese aquaculture, centered on the controversy between *Trachinotus anak* and *T. ovatus*, has persisted for several decades. In this study, 328 specimens of golden pompano were collected from 10 sampling sites in southern China, encompassing stocks from mariculture enterprises, local cage-culture farms, and the wild populations. The samples were identified based on morphological keys and cytochrome *c* oxidase subunit I (COI) reference sequences of important taxonomic works for *Trachinotus*. Of these, 326 individuals were morphologically identified as *T. anak*, characterized by a blade-like supraoccipital and inverted-L shape supraneurals. Only two individuals were identified as *T. blochii*, diagnosed by a tear-drop-shaped first supraneural. In phylogenetic analyses, all the analyzed *Trachinotus* sequences were clustered into 16 clades, corresponding to 16 valid species in genus *Trachinotus*. COI sequences of the 326 *T. anak* specimens were summarized into five haplotypes (Farm1–5), which form a well-supported clade with the *T. anak* reference sequences. Farm6, identified in two specimens, was resolved in the *T. blochii* clade. Additionally, we analyzed 58 COI sequences of *Trachinotus* species uploaded by Chinese researchers, whose haplotypes (Online1–9) were identified as *T. baillonii*, *T. blochii*, and *T. anak*. None of the Chinese *Trachinotus* sequences was included in the *T. ovatus* clade, suggesting that *T. ovatus*, the most commonly used name, is incorrect and should no longer be used for golden pompano in China. The holotype of *T. ovatus* was designated in 1896, which enforced the name to delegate a spotted Atlantic species. Taken together, our findings unequivocally support that the correct scientific name for golden pompano in China is *T. anak*.

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## 1 | Introduction

Golden pompano belongs to the genus *Trachinotus* Lacépède, 1801 of the Carangidae, which can be identified by its silvery, spotless body and falcated, yellowish-gray dorsal and anal fins. Artificial breeding of golden pompano in China can be traced back to the 1990s [1]. Taiwan first imported seedlings of golden pompano from Australia and achieved the breakthrough of its artificial breeding. Later, the species was introduced from Taiwan to Hainan in the early 2000s, where its artificial breeding earned remarkable success [2]. Due to the warmer climate, artificial breeding of golden pompano in Hainan has a longer breeding season and yields higher survival rates, making Hainan the main supplier of golden pompano fries for China's mariculture. The employment of deep-water cage farming technologies facilitated further expansion and upgrading of the industry. Today, golden pompano is the most productive fish in China's aquaculture, with its national breeding yield reaching 245,435 tons in 2022 [3]. Coastal water of Guangdong, Hainan, and Guangxi represent the core zone of golden pompano mariculture [1]. The high economic value of golden pompano has encouraged extensive research efforts in its genetics, physiology, and biology (e.g., [4–6]), aimed at improving the sustainability of its aquaculture. Nevertheless, multiple species names have been used in previous golden pompano studies, which account for severe taxonomic confusion. Further investigation is therefore needed to determine the correct species name for the cultivated gold pompano in China.

The controversy over the correct species name for golden pompano in China has persisted for decades. Cheng and Zheng [7] presented the first record of a *Trachinotus* species in China, which was identified as *T. blochii* (Lacepède, 1801). However, *T. blochii* was considered as a junior synonym of *T. ovatus* (Linnaeus, 1758) in their later work [8]. Many significant Chinese taxonomic works (e.g., [9, 10]) followed Cheng and Zheng's [8] view, thereby making *T. ovatus* the most common species name used in China. Later, Lin and Shao [11] reported *T. anak* Ogilby, 1909, *T. baillonii* (Lacepède, 1801), and *T. blochii* in Taiwan, and regarded records of *T. botla* (Shaw, 1803) and *T. ovatus* as misidentifications of *T. baillonii* and *T. blochii*, respectively. Zhang et al. [12] suggested two valid species among the cultivated golden pompano in China, namely *T. ovatus* and *T. blochii*, based on their external and skeletal morphology.

With the rise of golden pompano aquaculture, the debate and confusion over its scientific names further escalated. Although *T. ovatus* is the most commonly used name for golden pompano in Chinese aquaculture research (e.g., [4–6]), it is now considered a species restricted to the Atlantic [13]. Some recent studies argue that *T. anak* native to Australia is the true species cultivated in China [14, 15]. Wu and Zhong [16] proposed five *Trachinotus* species in China, viz. *T. anak*, *T. botla*, *T. baillonii*, *T. blochii*, and *T. mookalee* (Cuvier, 1832). Of these, *Trachinotus blochii* and *T. mookalee* were believed to be broadly cultivated in China, whereas *T. anak* was only distributed in the Taiwan Province. Moreover, Wu and Zhong [16] suggested that the broadly cultivated "*T. ovatus*" in China was actually *T. mookalee*. Recently, Li et al. [17] proposed that *T. anak* is clustered within the Indo-Pacific *T. ovatus*, proposing the former as a junior synonym of *T. ovatus*. Apparently, the correct scientific name for golden pompano has become a chronic controversy in China, which needs clarification to avoid any taxonomic confusion later on.

Smith-Vaniz and Walsh [13] performed a systematic review of the taxonomy of the genus *Trachinotus*, and their taxonomic views have been broadly accepted by many recent studies. The study summarized diagnostic characters and cytochrome *c* oxidase subunit I (COI) barcodes for 16 Indo-Pacific *Trachinotus* species, providing a robust reference for species identification within the genus. Under this framework, *T. ovatus*, which widely used in Chinese studies, was regarded as a spotted species restricted to the eastern Atlantic and absent from China. The other three candidate species for golden pompano, *T. blochii*, *T. mookalee*, and *T. anak* can be clearly distinguished using molecular markers and skeletal characters [13]. *Trachinotus mookalee* is diagnosed by the presence of a sausage-like supraoccipital bone. The first supraocular bone of *T. blochii* is swollen into a tear-drop shape. In contrast, the other two species possess inverted "L" shape supraoculars. Based on this taxonomic framework, 328 specimens of golden pompano were collected from 10 sampling sites in Guangdong and Hainan, China. Their skeletal characters and COI barcodes were compared with those reported by Smith-Vaniz and Walsh [13] to clarify the correct species name for the cultivated golden pompano.

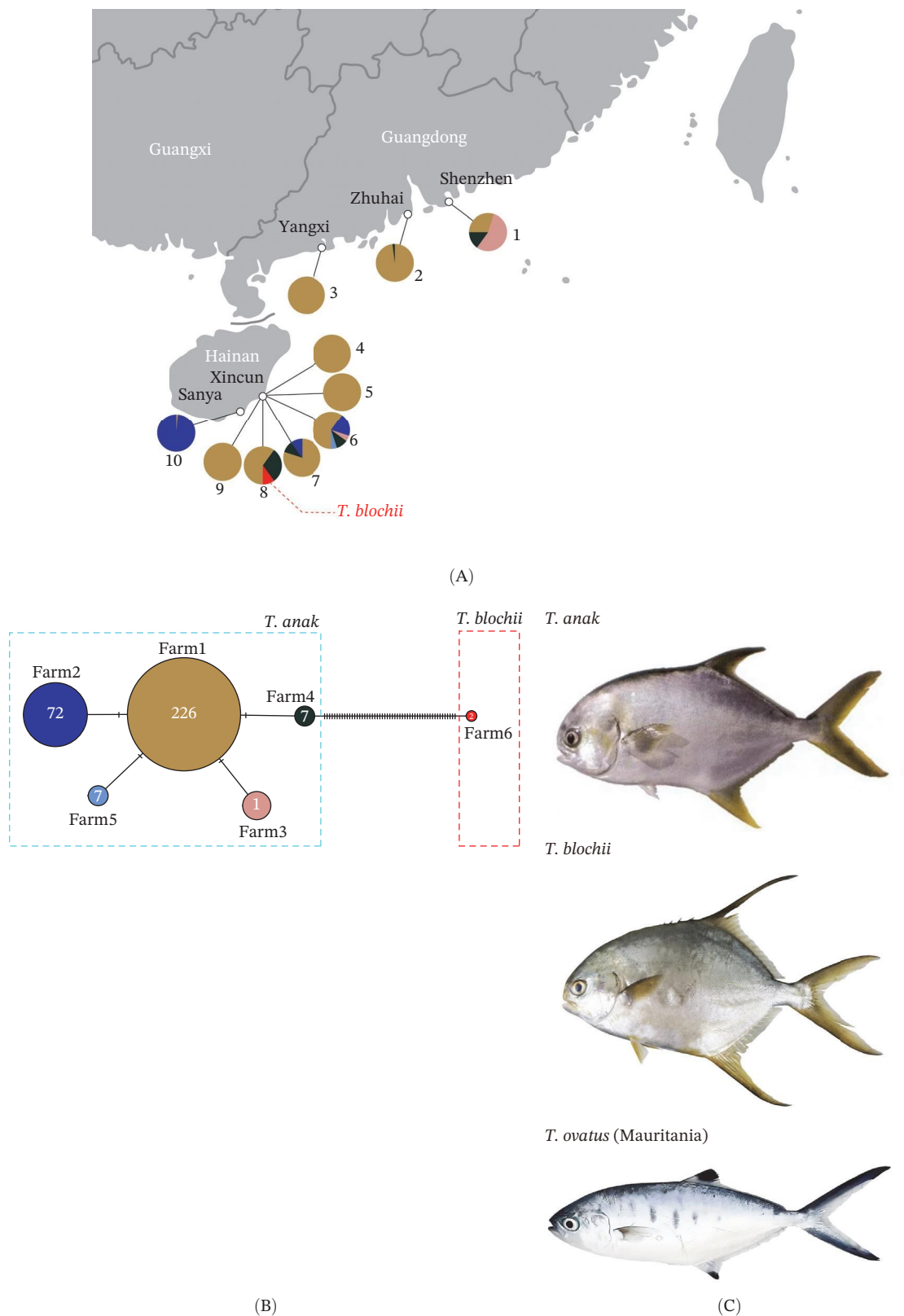
## 2 | Materials and Methods

### 2.1 | Sampling and Morphological Identification

In 2017 and 2019, 328 specimens of golden pompano were collected from Yangjiang, Shenzhen, Zhuhai, the Xincun Bay (Lingshui) and Sanya in Guangdong and Hainan provinces, China (sites 1–10; Figure 1), which represent the main provinces for golden pompano aquaculture in China. Among these locations, the Xincun Bay is one of the primary regions for cage mariculture and seedling production of golden pompano, benefiting from its warm climate and sheltered coastal structure. This inner bay hosts several leading enterprises in golden pompano aquaculture (e.g., Blue Ocean Co., Ltd., Chenhai Co., Ltd., and Qingli Co., Ltd.), which collectively supply the majority of seedlings for the golden pompano mariculture industry. Given its significant role, intensive sampling was conducted in the Xincun Bay, including specimens from three major enterprises, two local cage-culture farms, and its wild stock. Only the 67 individuals of site 10 were collected in 2017 from local cage-culture farm in Sanya, while those of the others were collected in 2019. Additionally, three specimens of *T. ovatus* (ovatus246–248) and *T. blochii* (blochii7–9) were respectively caught from the wild in Nouadhibou, Mauritania and Taiwan, China, for morphological comparison and molecular analyses. All specimens were at sub-adult stage, with their standard length ranging from ~15 to 30 cm. The specimens were carefully identified according to the morphological diagnoses given in Smith-Vaniz and Walsh [13], with particular attention to the supraoccipital and first supraocular bones. Pectoral fin clips were taken from the specimens and preserved in 95% ethanol for further experiments.

### 2.2 | Library Preparation, Resequencing, and Barcode Extraction

The COI barcodes used for molecular identification were extracted from the mitogenome data of all the *Trachinotus* specimens mentioned above. Whole-genome resequencing was



**FIGURE 1** | (A) A map showing sampling locations and haplotype compositions of the 10 golden pompano batches collected in this study: 1. Shenzhen Longqi Zhuang Co., Ltd.; 2. Zhuhai Hai Fa Co., Ltd.; 3. Hongyun Co., Ltd.; 4. Blue Ocean Co., Ltd.; 5. Chenhai Co., Ltd.; 6. Wild capture in the Xincun Bay; 7. Qingli Co., Ltd. 8. Local cage aquaculture farmer 1 (Xincun); 9. Local cage aquaculture farmer 2 (Xincun); 10. Local cage aquaculture farmer 3 (Sanya). (B) Haplotype network showing the genetic structure of the 328 golden pompano specimens collected in this study. Number of sequences for each haplotype were shown in the corresponding circles. (C) Photos of the three *Trachinotus* species collected in this research. Photo of *T. ovatus* is modified from fishbase database, under the approval of its author Oriol Ribalta.

employed to obtain mitogenome. All the genome extraction and sequencing experiments were performed by a commercial sequencing company BerryGenomics Co. Ltd. Total genomic DNA was extracted from pectoral fin clips of collected specimens using the TIANamp Marine Animals DNA Kit (DP324, TIANGEM Ltd.) following the manufacturer's instructions. The library of the extractions was prepared using Illumina TruSeq Nano DNA Sample Prep Kit (Illumina Inc.) following the manual instructions. The library was assessed using the TBS-380 Mini-Fluorometer (Turner BioSystems Inc.) and Picogreen (Invitrogen Ltd.), and then subjected to next generation sequencing on an Illumina Novaseq 6000 platform, generating 150-bp paired-end reads at an average sequencing depth of 10×. Low quality reads and adapters were removed from the raw reads using Illumina-trimomatic v0.36 (adapters.fa:2:30:10 SLIDINGWINDOW:4:15MINLEN:75 [18]). Mitogenomes were assembled from the clean data using the GetOrganelle pipeline (-R 10 -F animal\_mt [19]). The mitogenomes were further annotated using BLAST plugin in Geneious Prime v2024.0.5 (Biomatters Ltd., Auckland, New Zealand) to searches against *Trachinotus* mitogenomes on GenBank. COI barcodes of the collected specimens were then extracted from the mitogenomes by aligning with the reference barcodes reported by Smith-Vaniz and Walsh [13], using MAFFT v7.388 plugin in Geneious Prime with default settings [20].

### 2.3 | Haplotype Network and Phylogenetic Analyses

Information on all sequences used in this study is provided in Table 1 and Supporting information 1: Table S1. COI sequences of the 328 cultivated golden pompanos were identified by comparing with Smith-Vaniz and Walsh's [13] COI dataset using phylogenetic tree. This reference dataset including barcodes of the 16 *Trachinotus* species and two outgroups species, *Scomberoides commersonnianus* Lacépède, 1801 and *Lichia amia*. Additionally, four sequences from Sekar et al. [21] were also incorporated as reference sequences for *T. mookalee* (Table 1). For further comparison, 58 Chinese COI sequences of the *Trachinotus* species were also obtained from Genbank and Barcode of Life Data System (BOLD) for genetic comparisons (Supporting information 1: Table S1). To reduce computational time, haplotypes were separately generated for the Chinese sequences from this study and from online databases using DnaSP v6 (i.e., Farm1–6 and Online1–9, see Results [22]). Sequence alignment was performed using MAFFT v7.388 plugin in Geneious Prime with default settings [20]. Sequencing variation indices of the aligned dataset were calculated using DnaSP v6 [22].

To analyze genetic structure of the 328 golden pompanos, haplotype network of their COI sequences was assembled in PopART v1.7 (<http://popart.otago.ac.nz>) with the TCS algorithm and default settings [23]. For phylogenetic analyses, TPM3uf + I + G was selected as the best-fit model based on the Bayesian Information Criterion [24]. Maximum likelihood (ML) tree was inferred using IQ-TREE2 v2.3.6 [25], with node support assessed via 1000 ultrafast bootstrap replicates. For the Bayesian inference (BI) tree, two independent Markov chain Monte Carlo (MCMC) runs were performed in MrBayes v3.2, with four chains for 500,000 generations, sampling every 100 generations and

discarding the first 25% of samples as burn-in. Sufficient convergence of the MCMC runs was assessed based on summary statistics in MrBayes v3.2 ([26]; effective sampling size > 200, potential scale reduction factors ≈ 1). Both ML and BI trees were rooted by *S. commersonnianus*. ML and BI trees were visualized using Fig-Tree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

## 3 | Results

### 3.1 | Morphology of the Examined Pompano Specimens

All the 328 golden pompanos from the 10 sampling sites exhibited oval, spotless bodies, with blade-like supraoccipital bones (Figures 1C and 2). Among these, two individuals were identified as *T. blochii*, distinguished by more elongated falcate lobes on the dorsal and anal fins and tear-drop-shaped first supraneural bones (Figures 1C and 2B). Similarly, the three *T. blochii* specimens collected from coastal Taiwan displayed identical morphological traits to the two aquaculture individuals. The remaining 326 specimens have shorter falcated dorsal and anal fin lobes, and their first supraneural bone was in inverted “L” form (Figures 1C and 2C). Therefore, these golden pompano specimens can be morphologically identified as *T. anak* based on Smith-Vaniz and Walsh's [13]. Conversely, *T. ovatus* from Mauritania were characterized with fusiform and spotted body, less falcated dorsal and anal fin lobes, blade-like supraoccipital and inverted “L” shape first supraneural bone (Figures 1C and 2A).

### 3.2 | Dataset Used for Phylogenetic Analysis

All the COI barcodes obtained in this study, including the 328 golden pompanos and reference specimens of *T. ovatus* and *T. blochii*, have a sequence length of 650 bp. A total of six haplotypes (Farm1–6) were identified from the 328 golden pompanos collected in this study. Numbers of sequences identified as Farm1–6 were 226, 72, 7, 14, 7, and 2, respectively (Figure 1B). The 58 COI barcodes retrieved from GenBank and BOLD were summarized into nine haplotypes, namely Online1–9, with their sequence length ranging from 672 to 1551 bp. The numbers of sequences identified as Online1–9 were 5, 1, 2, 3, 1, 3, 3, 1, and 39, respectively. Due to their different sequence length and the lack of their exact sampling size, Online1–9 were not used for haplotype network inference. All the sequences generated in this study were deposited in NCBI GenBank under accession numbers of PV926773–PV926793 (Table 1).

The COI dataset for tree reconstruction comprised of 65 sequences (Table 1): 40 sequences from Smith-Vaniz and Walsh [13]; four sequences from Sekar et al. [21]; six haplotypes (Farm1–6) summarized from 328 golden pompanos collected in this study; 9 haplotypes (Online1–9) generated from 58 *Trachinotus* COI barcodes upload to Genbank and BOLD by Chinese studies, respectively; three *T. ovatus* sequences from coastal Mauritania (ovatus246–248); three *T. blochii* from northern Taiwan, China (blochii7–9). The dataset was aligned and trimmed into a 650-bp alignment, with 179 polymorphic sites, 149 parsimony informative sites, and 1.81% missing data (i.e., external gaps).



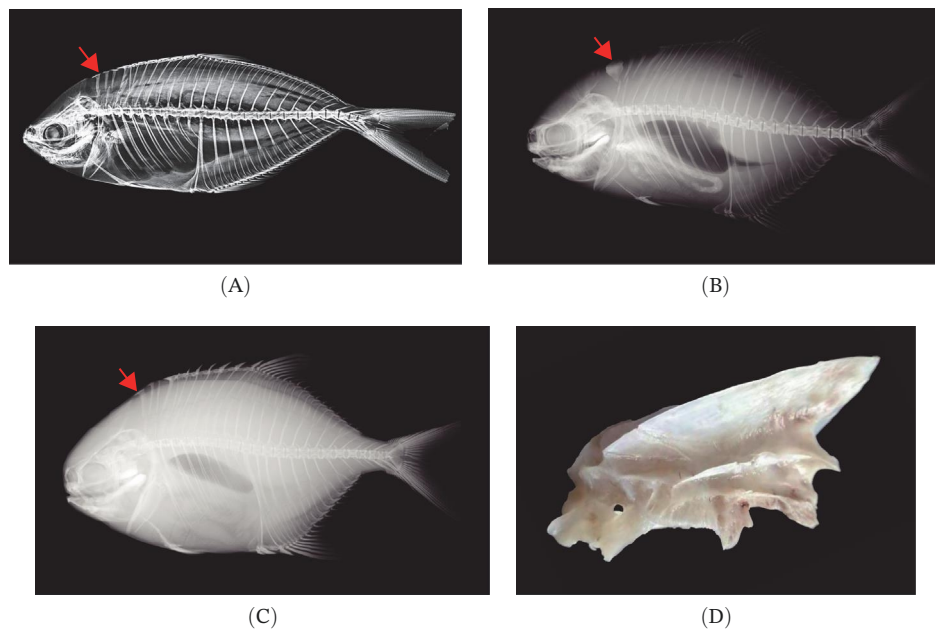
**TABLE 1** | COI sequences used for phylogenetic analysis in this study.

| Sources                    | Species                                              | BOLD/NCBI                                                                        |
|----------------------------|------------------------------------------------------|----------------------------------------------------------------------------------|
| Smith-Vaniz and Walsh [13] | <i>T. africanus</i> Smith, 1967                      | FOAH846-08; JF494715                                                             |
|                            | <i>T. anak</i> Ogilby, 1909                          | FOAC409-05                                                                       |
|                            | <i>T. baillonii</i> (Lacepède, 1801)                 | DBMF107-10; FOAC408-05; FTWS199-09; MBFA763-07; SAIAB486-06                      |
|                            | <i>T. blochii</i> (Lacepède, 1801)                   | FOAC411-05; SAIAB448-06                                                          |
|                            | <i>T. bolta</i> (Shaw, 1803)                         | TZMSC538-06; TZMSC524-05                                                         |
|                            | <i>T. carolinus</i> (Linnaeus, 1766)                 | BCOLL389-08; SMSA486-09                                                          |
|                            | <i>T. coppingeri</i> Günther, 1884                   | FOAC406-05; FOAD511-05; FOAD515-05                                               |
|                            | <i>T. falcatus</i> (Linnaeus, 1758)                  | LIDM1349-08; MLIII368-08; MLIII196-08                                            |
|                            | <i>T. goodei</i> Jordan and Evermann, 1896           | MXV148-11; MXV149-11                                                             |
|                            | <i>T. goreensis</i> Cuvier, 1832                     | BAFEN355-10; BAFEN357-10                                                         |
|                            | <i>T. macrospilus</i> Smith-Vaniz and Walsh, 2019    | MARQ384-12; MARQ385-12                                                           |
|                            | <i>T. mookalee</i> Cuvier, 1832                      | GBMIN119993-17; GBMIN124842-17<br>GBMIN130195-17                                 |
|                            | <i>T. ovatus</i> (Linnaeus, 1758)                    | MLFPI019-09; GBGC1144-06; BIM405-15                                              |
|                            | <i>T. paitensis</i> Cuvier, 1832                     | ANGBF1237-12                                                                     |
|                            | <i>T. rhodopus</i> Gill, 1863                        | RDFCA397-05                                                                      |
|                            | <i>T. stilbe</i> (Jordan & McGregor, 1898)           | LIDMA1275-12                                                                     |
|                            | <i>Lichia amia</i> (Linnaeus, 1758)                  | DNATR812-13                                                                      |
|                            | <i>Scomberoides commersonnianus</i> (Lacepède, 1801) | DBMF064-10                                                                       |
|                            | <i>T. mookalee</i> Cuvier, 1832                      | KU296860; KU296861;<br>KU296862; KU296864                                        |
|                            | <i>T. anak</i> Ogilby, 1909                          | Farm1–5: PV926773–PV926777<br>Online5–9: PV926783–PV926787                       |
| This study                 | <i>T. blochii</i> (Lacepède, 1801)                   | Farm6: PV926778<br>Online3–4: PV926781–PV926782<br>Blochii7–9: PV926791–PV926793 |
|                            | <i>T. baillonii</i> (Lacepède, 1801)                 | Online1–2: PV926779–PV926780                                                     |
|                            | <i>T. ovatus</i> (Linnaeus, 1758)                    | Ovatus246–248: PV926788–PV926790                                                 |
|                            |                                                      |                                                                                  |

### 3.3 | Haplotype Network, Phylogenetic Inference, and Species Identification

In haplotype network (Figure 1B), the six haplotypes were clustered into two groups, that is, Farm1–5 and Farm6, with 53 bp of fix differences between groups. 68% of the collected golden pompano were identified as Farm1, which was also the dominant haplotype for sites 2–9 (collected in 2019). To the contrary, site 1 (Longqi Zhuang Co., Ltd., Shenzhen, 2019) and site 10 (Local cage-culture farm3, Sanya, 2017) were dominated by Farm3 and Farm2, respectively (Figure 1A). However, only 1–2 bp pairwise difference was found among Farm1–6, suggesting their low-level of differentiation (Figure 1B).

In the ML and BI trees, the *Trachinotus* sequences were resolved as 16 well-supported monophyletic groups (posterior probability [PP]=0.97–1, Bootstrap value [BS]=96–100, Figure 3), corresponding to the 16 species used in Smith-Vaniz and Walsh [13]. Farm1–5 were nested within the *T. anak* clade, which comprised of 326 golden pompanos from the Chinese aquaculture farms. Farm6 was included in the *T. blochii* clade, corresponding to the two aquaculture specimens with tear-drop like first supra-neural bone, which were collected from local aquaculture farmer 2 of the Xincun Bay (Figure 1A). For haplotypes identified from Genbank and BOLD sequences, Online1–2 was resolved in the *T. baillonii*. Online3–4 and Online5–9 were placed in the



**FIGURE 2** | X-ray photos of *T. ovatus* (A), *T. blochii* (B), *T. anak* (C), Their first supraneural is indicated by red arrows. The blade-like supraoccipital of *T. anak* (D) is shown.

*T. blochii* and *T. anak* clades, respectively. Five spotless Indo-Pacific species, that is, *T. africanus* Smith, 1967, *T. blochii*, *T. falcatus* (Linnaeus, 1758)], *T. mookalee* and *T. anak*, formed a monophyletic group, although supported by low BS and PP values of 65 and 0.74. *T. blochii* was well supported as the sister species of *T. africanus* (PP = 1, BS = 99), while *T. anak* was sister to *T. mookalee* (PP = 1, BS = 99, Figure 3). Most spotted species constituted a well-supported clade (i.e., *T. baillonii*, *T. coppingeri*, *T. ovatus*, *T. macrospilus*, and *T. botla*, PP = 1, BS = 98), except that *T. goreensis* was resolved as the outermost branch of the genus *Trachinotus* in ML tree (BS = 53).

## 4 | Discussion

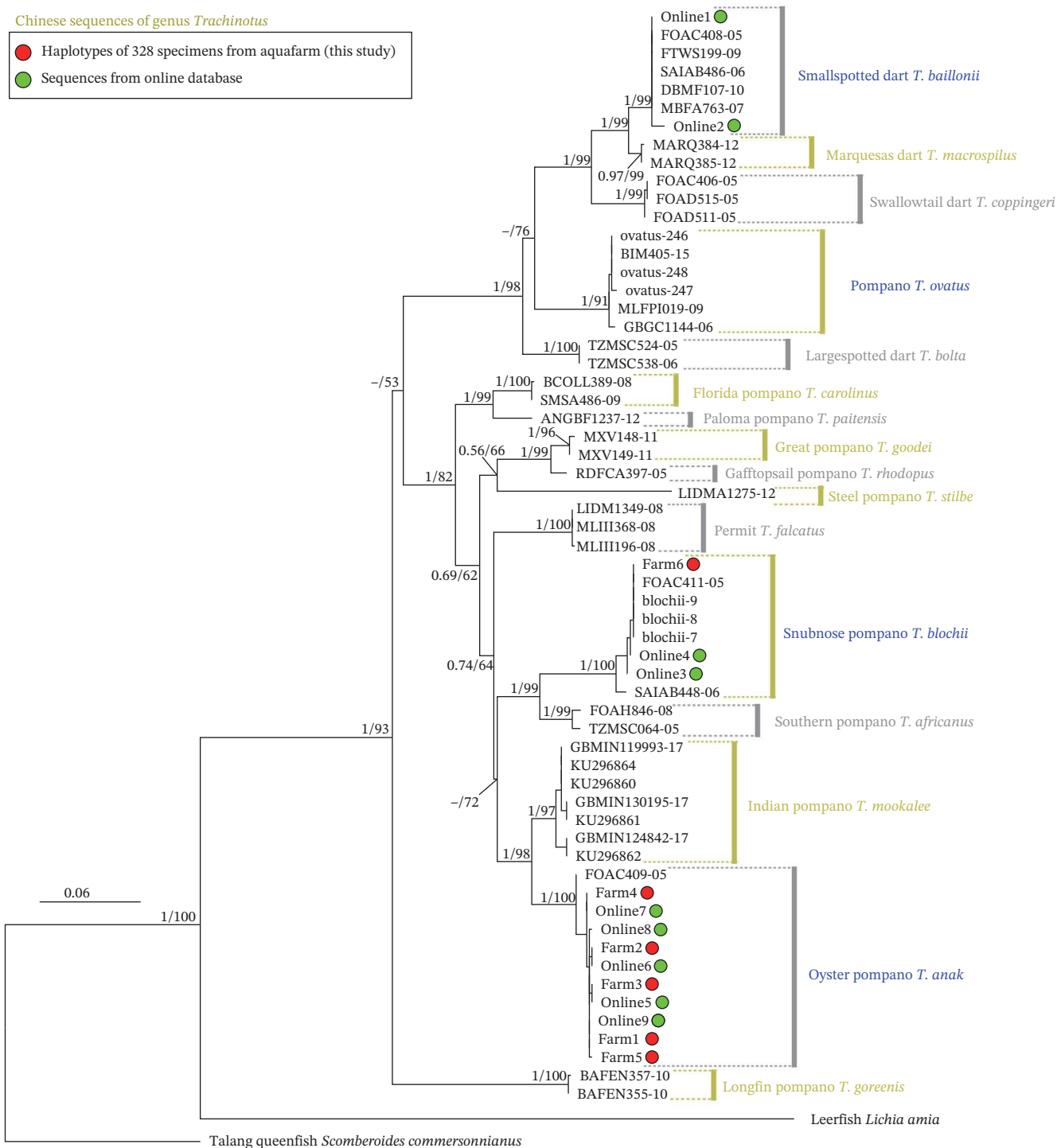
### 4.1 | *T. anak* Is the Correct Scientific Name for Golden Pompano in China's Aquaculture

In this study, most of the cultivated golden pompanos collected in Guangdong and Hainan were morphologically and genetically identified as *T. anak*, which clearly supported *T. anak* as the proper species name of golden pompano (Figures 2C and 3). Previous studies believed that there are two *Trachinotus* species in China's aquaculture [11, 12]. Our results also indicated two species among the 328 collected samples (Figure 3), which, based on identification keys and sequences from Smith-Vaniz and Walsh [13], were *T. anak* and *T. blochii*. 326 individuals of the collected golden pompanos have an inverted-L-shaped supraneural bone and should be identified as *T. anak* (Figures 1 and 2). China's mariculture of golden pompano is believed to have started in Taiwan. The species was then introduced to Guangdong and Hainan for cage aquaculture in 1992, which has become the most productive fish species in China [2]. The Fish Database of Taiwan (<https://fishdb.sinica.edu.tw/>) stated that *T. anak* was introduced from Australia to Taiwan for mariculture. These historical records, together with our molecular and

morphological results, strongly support that golden pompano cultivated in China, in most cases, is *T. anak*.

*T. blochii* is naturally distributed in the West Pacific [11, 27], but it appears to be rare in China's aquaculture. Only two *T. blochii* specimens were recorded from a local cage-culture farmer of Xincun, diagnosed by their blade-like supraoccipital and the tear-drop-shaped first supraneural, supporting rarer presence of *T. blochii* in the golden pompano broodstock (Figures 1A and 2B) [12, 13]. Some local cage-culture farmers in China often collect golden pompano fries from wild stock for mariculture, which might occasionally introduce *T. blochii* into their culture stocks (personal observation). Additionally, artificial hybrids between *T. blochii* and *T. anak* (e.g., Chenhai No. 1 by Chenhai Co. Ltd.) have been developed for mariculture, which could account for gene flow between the two species [28, 29]. However, given the presence of the tear-drop-shaped first supraneural, it is more likely that the two individuals were pure *T. blochii* occasionally introduced to mariculture.

*Trachinotus ovatus* (originally, *Gasterosteus ovatus* Linnaeus, 1758) was first described in Linnaeus [30] with its type locality noted as Asia, but the whereabouts of its holotype were unclear after its publication. The description of *T. ovatus* can be applied to multiple species, making species taxonomy of genus *Trachinotus* controversial in several works. Of these works, Günther [31] treated many species names (e.g., *T. mookalee*, *T. blochii*, and *T. falcatus*) as junior synonyms of *T. ovatus*, which had affected many significant Chinese studies on pompano (e.g., [8, 12]). Resultantly, *T. ovatus* has been taken as a species broadly distributed in the Indo-Pacific region, especially in China, where golden pompano has thrived into the most productive species in China's aquaculture industry. Additionally, the type locality Asia provided by Linnaeus [30] was also considered as the evidence to determine identity of *T. ovatus* (e.g., [17]). Nevertheless, the type locality given by Linnaeus [30] is now considered incorrect. The holotype (ZIU202) for *G. ovatus* had been designated from



**FIGURE 3** | ML tree of genus *Trachinotus* reconstructed from COI sequences. Posterior probabilities (before diagonal) and bootstrap values (after diagonal) obtained in BI and ML analyses are shown on each node, hyphen indicates that such node is not indicated in BI or ML tree. Chinese and scientific names of each species are shown for the Chinese researcher's reference.

Linnaeus's collection in the Museum of Uppsala University by Lönnberg [32]. Wheeler, through his series of studies on Linnaeus's collection worldwide [33, 34], has confirmed that this holotype is the only known specimen noted as *G. ovatus* by Linnaeus. According to the Principle of Typification, holotype, once fixed, is the only objective standard for the application of the name it bears (Article 61, the International Code for Zoological Nomenclature, <https://code.iczn.org>). The holotype of *T. ovatus* is a spotted pompano species only found in Atlantic (figure 2 in

[34]), which consequently enforces the name to delegate the Atlantic species. The holotype of *T. ovatus* has been accepted by multiple recent studies [35, 36]. Therefore, *Trachinotus ovatus* should no longer be used for golden pompano in China.

#### 4.2 | Is *T. anak* Naturally Distributed in China?

Although the identity of golden pompano has been clarified, it remains uncertain whether *T. anak* is naturally distributed in

China. In 1950–1980s, the ichthyologists recognized only one unspotted *Trachinotus* species in China (noted as either *T. blochii* or *T. ovatus* [7, 8]). In 1990s, *Trachinotus anak* was introduced from Australia to Taiwan, China, which is later introduced to Guangdong, Hainan, and Fujian Province [2]. At this time, several works began to report two unspotted *Trachinotus* species in China, viz., *T. blochii* and *T. anak* (or noted as *T. ovatus* [11, 12]). Lin and Shao [11] suggested that *T. anak* was an occasional species, but it is now commonly found in coastal China. A similar pattern was observed in Japan, *T. blochii* used to be the only unspotted pompano species in Japan [27]. Presences of *T. mookalee* and *T. anak* in Japan are only reported by works after 1990s [37, 38]). Apparently, emergence of *T. anak*'s record in the North-west Pacific area showed coincidence with the onset of its aquaculture in China, which might hint *T. anak* as an alien species from Australia. *Trachinotus anak* has been broadly cultivated and utilized as a stocked species to increase wild fishery resources [39]. Artificial releases and unintentional escape from aquaculture facilities might have facilitated establishment of its wild population in the Northwest Pacific. In this study, only five haplotypes differing by 1–2 bp, were identified from the 326 *T. anak* specimens, while most stocks collected in 2019 were dominated by haplotype Farm1 (Figure 1A), suggesting reduced genetic diversity and possible inbreeding in China's *T. anak* mariculture stocks. Notably, although the site 6 stock was collected from the wild of the Xincun Bay, its haplotype composition was similar to the adjacent mariculture stocks (Figure 1A). This pattern suggests that aquaculture escape may contribute to the wild *T. anak* population in the Xincun Bay, potentially homogenizing the genetic structure between wild and cultured stocks. Is *T. anak* naturally distributed in China? It still requires more historical collection (e.g., 1950–1980s) to clarify this issue.

### 4.3 | Some Comments to Evolution of Genus *Trachinotus*

To date, a comprehensive evolutionary hypothesis is still not available for the genus *Trachinotus*, primarily due to the lack of a complete phylogenetic analysis encompassing all 21 recognized species. The *Trachinotus* species could be superficially divided by body marking—the spotted, striped, and unspotted groups. The spotted group contains seven species: *T. ballonii*, *T. botla*, *T. coppingeri*, *T. macrospilus* Cuvier, 1832, *T. goreensis*, *T. marginatus* Cuvier, 1832, and *T. ovatus*. The striped group includes *T. rhodophus* and *T. goodei*, while the other 11 species have neither stripe nor spot on body [13, 40, 41]. Such difference in body markings might reflect their phylogenetic relationship. Our study recovered a monophyletic group comprised of five spotted species, *T. ballonii*, *T. botla*, *T. coppingeri*, *T. macrospilus*, and *T. ovatus*, which is sister to the clade of all the unspotted and striped species (Figure 3). Similar topologies were also retrieved in Smith-Vaniz and Walsh [13] and Glass et al. [42]. This implies that the spotted and non-spotted species might have evolved separately since the early evolutionary history of the genus. Compared with most *Trachinotus* species, these five spotted species have more elongated body and preferred shallow waters of the surf zones, which might also support their monophyly. Another spotted species, *T. goreensis*, was resolved as the outermost species, suggesting that the ancestor of *Trachinotus* might also have a spotted body. In the sister clade of *Trachinotus*, *Lichia* Cuvier,

1816 and *Scomberoides* Lacépède, 1801 were also characterized by having spots on body, while the unspotted *Oligoplites* Gill, 1863 diverged with *Scomberoides* in the Miocene [42]. This implies that the common ancestor of these four genera might also have a spotted body, unspotted body is a more derived character. Furthermore, hyperostosis occurs regularly in lacrimal, ribs, supraneural, supraoccipital, and dorsal-fin pterygiophores of large adults of *T. africanus*, *T. anak*, *T. blochii*, *T. kennedyi* Steindachner, 1876, *T. falcatus*, *T. marginatus*, *T. maxillosus*, and *T. mookalee* [43, 44], with six of them grouped into a single clade in phylogenetic trees (Figure 3; [13, 42]). Hyperostosis of these bones might also imply phylogeny of the *Trachinotus* species. Does body marking, habitat preference, and hyperostosis reflect the phylogeny of *Trachinotus*? These hypotheses remain further verification with a more complete phylogenetic framework of the 21 *Trachinotus* species.

Similar to many carangids, *Trachinotus* exhibits a broad geographic distribution across coastal waters of temperate and tropical regions. Glass et al. [42] indicated that *Trachinotus* might have a Mid-Miocene origin, when the tropical Atlantic, Pacific and Indian Oceans were well connected by the Central American Seaway and Tethys Seaway [45]. The well connectivity among oceans might allow global dispersal of *Trachinotus*, leading to its global distribution. Conversely, closure of these two significant seaways could greatly impact the evolution of *Trachinotus*, leading to isolation and divergence. In fact, the distribution of *Trachinotus* can be delineated into four biogeographical areas based on species composition: the East Pacific, Indo-West Pacific (including tropical islands of the central Pacific), West Atlantic, and East Atlantic (Supporting information 2: Table S2). No shared species is found between any two areas, suggesting strong isolation among areas for *Trachinotus*. The Atlantic species *T. ovatus* is resolved as the sister of three Indo-Pacific species, *T. ballonii*, *T. macrospilus*, and *T. coppingeri*, suggesting possible Trans-Tethyan divergence among these species. Across the Isthmus of Panama, two pairs of sister species can be found in either side of the Americans, that is, *T. goodei* and *T. rhodophus*, *T. carolinus*, and *T. paitensis* (Figure 3). Their divergence time was dated back to the Pliocene [42]. These divergence patterns suggests that the closure of the Isthmus in late Pliocene might cause allopatric speciation of *Trachinotus*, which might play a key role in shaping its biogeographic pattern in the Americas [46]. The Sunda Shelf, exposed in the Quaternary Glacial Periods, is a well-known barrier to cause trans-oceanic divergence between species of the Indian and Pacific Oceans [47]. *Trachinotus mookalee* and its sister *T. anak* inhabit the Indian and Pacific Oceans, respectively, with their divergence time dated back to the Quaternary Period [42]. While geographic distributions provide clues to the formation of certain *Trachinotus* sister species, the origin and dispersal route of the genus as a whole are still poorly understood. A comprehensive phylogenetic tree encompassing all 21 species is essential for reconstructing their ancestral distribution and developing a reliable theory for the evolution of *Trachinotus*.

## 5 | Conclusion

There has been a decades-long debate whether *T. anak* or *T. ovatus* should be the correct scientific name of cultivated golden pompano in China. In this study, 328 cultivated golden



pompanos were collected from 10 sampling locations in southern China. Of these, 326 individuals were morphologically identified as *T. anak*, characterized by a blade-like supraoccipital and inverted-L shape supraneurals. Only two individuals were identified as *T. blochii*, diagnosed by a tear-drop-shaped first supra-neural. In the COI phylogenetic tree, all the analyzed *Trachinotus* sequences were clustered into 16 clades, corresponding to 16 valid *Trachinotus* species. Five haplotypes (Farm1–5), summarized from the 326 *T. anak* specimens, were nested within the *T. anak* clade. The haplotype of the two *T. blochii* specimens (Farm6) was placed in the *T. blochii*'s clade. Additionally, nine COI haplotypes (Online1–9) were obtained from 58 *Trachinotus* sequences uploaded by Chinese researchers. They were identified as *T. baillonii* (Online1–2), *T. blochii* (Online3–4) and *T. anak* (Online5–9). No *T. ovatus* sequence was found in China, suggest this species is never presents in China. The holotype of *T. ovatus* has been designated in 1896, which enforced the name to represent a spotted Atlantic species, despite the type locality Asia proposed in Linnaeus [30]. Conclusively, *T. ovatus* is not distributed

in China, and should no longer be used for golden pompano in China. In our samples, most cultivated golden pompanos were *T. anak*, while only two were *T. blochii*. This unequivocally supports that *T. anak* is the main species in China's aquaculture, which thus should be the correct scientific name for golden pompano. We recommend its formal adoption in future research, aquaculture practices, and regulatory documentation. However, it remains unclear if *T. anak* is naturally distributed in China. Only a single unspotted species was recorded in the Northwest Pacific by works before 1990s (noted as either *T. blochii* or *T. ovatus*), while presences of *T. anak* are all reported after the onset of its aquaculture in this area. *T. anak* could be an alien species introduced from Australia, but it requires more museum specimens for further verification. Based on current phylogenetic research, our study proposed that morphological traits, habitat preferences, and historical biogeographic events are likely to shape evolution of the genus *Trachinotus*. The spotted *Trachinotus* species, as well as those with hyperostosis, tend to form monophyletic group within phylogenetic tree. Geographic isolation driven by seaway closures and glacial barriers has likely contributed to speciation across oceanic regions. However, many spotted and hyperostotic species have not been included in current phylogenetic studies. A comprehensive phylogenetic tree of all the 21 *Trachinotus* species is crucial for testifying the proposed hypotheses in the future.

#### Author Contributions

Jiehong Wei and Liang Guo conceived and designed the study. Liang Guo, Jing Liu, Laith A. Jawad, Nawzet Bouriga, and Adel A. Basyouny Shahin conducted the investigation and sampling. Jiehong Wei and Liang Guo performed the molecular experiments. Jiehong Wei performed the analyses and wrote the manuscript draft. Liang Guo and Jing Liu provided funding support.

#### Acknowledgments

The authors would like to thank Prof. Ronald Fricke of the Staatliches Museum für Naturkunde Stuttgart for his invaluable help in interpretation of the ICZN codes. We also acknowledge Ms. Guan-Chen Liu of the

National Sun Yat-Sen University for her help in collecting *T. blochii* specimens from the Taiwan island.

#### Funding

The work was supported by the National Science Foundation of China (Grant number: 32270472), National Key R&D Program of China (Grant number: 2024YFD2401802), the Guangdong Basic and Applied Basic Research Foundation (Grant number: 2019A1515110309), and the Natural Science Foundation of Hainan Province (Grant number: 320QN362).

#### Disclosure

All authors significantly contributed to the drafts, finalized the manuscript, and provided their approval for publication.

#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

The COI sequences generated in this study (i.e., Farm1–6, Online1–9, ovatus246–248, and blochii7–9) were deposited on the NCBI GenBank, under accession number of PV926773–PV926793.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.

**Supporting Information 1.** Table S1. GenBank- and BOLD-derived COI sequences used to generate haplotypes Online1–9.

**Supporting Information 2.** Table S2. *Trachinotus* species and their distributions based on Eschmeyer's Catalog of Fishes (Frick et al. 2024).