Received: 23 January 2019 | Revised: 6 May 2019 | Accepted: 22 May 2019

DOI: 10.1111/zsc.12366

ORIGINAL ARTICLE

Zoologica Scripta | WILEY

Evolutionary aspects of cephalic sensory papillae of the Indo-Pacific species of *Eleotris* (Teleostei: Eleotridae)

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Funding information
National Museum of Natural History; AIMARA Association; French Ichthyological Society; JSPS KAKENHI, Grant/Award Number: 16K07492

Abstract

Eleotris species (Teleostei: Eleotridae) are one of the most common fish in Indo-Pacific estuaries and insular freshwater streams. In these rivers, they are a sit-and-wait predator. They have an amphidromous life cycle, *that is* adults grow, feed and reproduce in rivers, while larvae have a marine dispersal phase. Larvae recruit back to rivers and settle in stream habitats. Primary characters used to determine *Eleotris* species are the presence and the disposition of cephalic sensory papillae rows on the operculum and under the eyes as well as scale row numbers. The morphology of these cephalic sensory papillae is of particular importance in this predatory genus as it is generally correlated in fish to predation and feeding. In this paper, we have established a molecular phylogeny of the genus based on the 12 mitochondrial protein-coding genes to discuss the relationship between Indo-Pacific *Eleotris* species. There is a well-supported dichotomy in the molecular phylogeny, and this separation into two main clades is also morphologically visible, as it reveals a difference in the arrangement of cephalic sensory papillae. Indeed, the phylogeny distinguishes the species with the "open" pattern of the operculum sensory papillae and the species with the "closed" one. This phylogeny thus reflects the morphology of the opercular papillae. The evolution of this character is discussed in terms of the adaptation of the *Eleotris* genus to life in tropical insular river systems.

1 | INTRODUCTION

Insular freshwater systems in the Indo-Pacific area are known to be perilous habitats because they are subject to extreme climatic and hydrological seasonal variations such as drought or cyclonic flood events. They are inhabited by gobioids with a fascinating life cycle adapted to the ecological conditions prevailing in these distinctive habitats (Keith, 2003). To colonise these rivers, species have developed a specific life cycle called amphidromy (Closs & Warburton, 2016). Whether endemic, or more broadly distributed, amphidromous species spawn in freshwater and the free embryos drift downstream to the sea where they undergo a planktonic phase for several months (McDowall, 2007). After this marine phase, individuals return to rivers to grow and reproduce (Keith et al., 2008; McDowall, Mitchell, & Brothers, 1994). With the marine larval phase, amphidromous species are able to disperse and colonise new and remote islands (Keith, 2003). They are the biggest contributors to the diversity of the freshwater communities in Indo-Pacific islands (Keith, Lord, & Maeda, 2015).

Among amphidromous fishes, the genus *Eleotris* (Teleostei: Eleotridae) is one of the most common in Indo-Pacific estuaries and insular freshwater streams (Mennesson, Tabouret, Pécheyran, Feunteun, & Keith, 2015). In these rivers, it is a sit-and-wait predator characterised by a distinctive eleotrid morphology—moderately blunt large head, torpedo-like body form, broad, rounded caudal fin and prominent lower jaw (Pezold & Cage, 2002). It lives close to the riverbank where the current is slow, or in the lentic zones (Keith, Marquet, Lord, Kalfatak, & Vigneux, 2010). Although adult *Eleotris* species are not, in most places, targeted as a food resource, they are however targeted for human consumption at

the postlarval stage as they recruit back to rivers. *Eleotris* species are hence likely an important component of the structure and functioning of these subtropical and tropical islands ecosystems, both as predators and as a food source with postlarvae fisheries (Nordlie, 1981; Perrone & Vieira, 1991; Pezold & Cage, 2002). Nevertheless, several species are threatened and endangered (Mennesson, Bonillo, Feunteun, & Keith, 2018).

It is well known that field identification of *Eleotris* species is difficult due to the lack of meristic characters without overlap (Pezold & Cage, 2002) and because all the species are generally brown and look alike (Mennesson, 2016). Akihito (1967) demonstrated the significance of the free neuromast patterns on the head to diagnose species. Later, Miller (1998) reviewed *Eleotris* species from the eastern Atlantic and Pezold and Cage (2002) from the eastern Pacific and western Atlantic. They found cephalic free neuromast patterns and differences in squamation to be the most useful characters in separating species. Recently, in her revision of this genus in the Indo-Pacific area, Mennesson (2016) validated the diagnostic utility of the presence and disposition of cephalic sensory papillae rows on the operculum and under the eyes. She distinguished five different patterns of row arrangement for the known species.

The morphology of these cephalic sensory papillae is of particular importance in this predatory genus as it is generally correlated in fishes to predation and feeding. Fish free neuromasts have been described as playing a complementary role to vision in feeding behaviour (Disler, 1971; Iwai, 1972a, 1972b). Indeed, in some species, free neuromasts play a major role in detecting prey (Mukai, Yoshikawa, & Kobayashi, 1994).

Despite the growing interest in their ecological roles in freshwater and estuarine communities, little attention has been given to the evolution and the phylogeny of this genus, particularly in accordance with the pattern variations of the cephalic sensory papillae. The aim of this paper is to resolve the phylogenetic relationships between the Indo-Pacific species of *Eleotris*. The exploration of these relationships will be done on the one hand by using partial cytochrome oxydase I mitochondrial gene, and on the other hand, using the complete mitochondrial genome. This last analysis will enable us to discuss on the contribution of the mitogenomic information to the resolution of the molecular phylogeny of the *Eleotris* genus in accordance with the main diagnostic characters used in taxonomy, the arrangement of cephalic sensory papillae rows.

2 | MATERIALS AND METHODS

2.1 | Sample collection

The fish used for the study were collected from Indian and Pacific island freshwater streams. Individuals were sampled using a DEKA 3000 electrofishing system (Gerätebau), or using a hand net without the electrofishing system. Following annex IV of the directive 2010/63/EU, fish were either euthanised using an overdose of clove oil (10%), or a piece of fin was taken while the fish was anaesthetised. In the case of anaesthetisation, the fish was then awakened in clear water before it was released. Entire fish or fin clips were stored and preserved in 95% or 99% alcohol for molecular analysis. A total of 128 *Eleotris* specimens were studied. Species, specimens and localities sampled are listed in Table 1.

Specimens were compared to type specimens from Museum collections (MNHN: Muséum national d'Histoire naturelle, Paris; RMNH: Rijksmuseum van Natuurlijke Historie, Leiden; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZMH: Zoological Museum Hamburg; BMNH: Natural History Museum, London; CAS-SU: California Academy of Sciences (San Francisco), Stanford University (Palo Alto, California); WAM: Western Australian Museum, Perth, Western Australia; SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt).

2.1.1 | Material examined

Eleotris oxycephala Temminck & Schlegel, 1845: 1 possible type from Japan (BMNH 2015.4.8.1). *Eleotris balia* Jordan & Seale, 1905: holotype from China (USNM 52082). *Eleotris sandwicensis* Vaillant & Sauvage, 1875: syntypes from Hawaiian Islands (MNHN 271-6-19-3, MNHN 271-6-19-4). *Eleotris acanthopoma* Bleeker, 1853: holotype from Sumatra, Indonesia (RMNH 25934). *Eleotris melanosoma* Bleeker, 1853: 1 syntype from Sumatra (or Ceram), Indonesia (RMNH 4815) (Synonyms: *Eleotris soaresi* Playfair, 1867: syntypes from Mozambique, Africa [BMNH 1856.3.18.26-27]. *Eleotris pseudacanthopomus* Bleeker, 1853: holotype from Western Sumatra, Indonesia [SMNS 10595]. *Culius macrocephalus* Bleeker 1857: holotype from Buru, Indonesia [RMNH 4757]. *Culius insulindicus* Bleeker, 1875: syntypes from Sumatra, Indonesia [RMNH 4804]. *Culius macrolepis* Bleeker, 1875: syntypes from Ambon, Indonesia [RMNH 4759]). *Eleotris bosetoi* Mennesson, Keith, Ebner, & Gerbeaux, 2016: holotype from Solomon Islands (MNHN 2015-0382); paratypes from Solomon Islands (MNHN 2015-0380, MNHN 2015-0379, MNHN 2016-0001). *Eleotris fusca* (Bloch & Schneider), 1801: no type known (Synonyms: *Eleotris niger* Quoy and Gaimard, 1824: 1 syntype from Waigeo, Indonesia [MNHN A-1578]. *Eleotris vitianus* Sauvage, 1880: syntypes from Fiji Islands [MNHN A-1420]. *Eleotris fornasini* Bianconi, 1857: holotype from Mozambique, Africa [BMNH 1852.9.13.179]. *Eleotris andamensis* Herre, 1939: paratypes from Andaman Islands [CAS-SU 37152]). *Eleotris klunzingerii* Pfeffer, 1893: holotype from Zanzibar, Africa (ZMH-H412). *Eleotris eigenmanni* Popta, 1921: 1 lectotype? from Sunda Islands, Indonesia (SMF 6594); paralectotypes from Sunda Islands, Indonesia (SMF 6595-99). *Eleotris vomerodentata* Maugé, 1984: 1 holotype

TABLE 1 Details of tissue samples of *Eleotris* specimens used in the study

Species	Locality	*N*	*N* total	*COI*	*N* total	Partial mtDNA	*N* total
E. oxycephala	Japan	3	3	2	2	2	2
E. sandwicensis	Hawaii	1	1	1	1	—	—
E. mauritiana	Seychelles	7	15	7	15	2	2
	Reunion	2		2		—	
	Maurice	1		1		—	
	Mayotte	2		2		—	
	Madagascar	3		3		—	
E. acanthopoma	Moorea	2	8	2	8	—	—
	Rarotonga	1		1		—	
	Vanuatu	2		2		—	
	Solomon	2		2		—	
	Pohnpei	1		1		—	
E. melanosoma	Solomon	5	16	5	16	3	8
	Philippines	1		1		1	
	Moorea	1		1		—	
	Okinawa (Japan)	4		4		1	
	Mayotte	2		2		—	
	Vietnam	3		3		3	
E. bosetoi	Solomon	5	5	4	4	2	2
E. fusca	Marquesas	2	52	2	32	—	24
	Rurutu	4		3		1	
	Rarotonga	4		2		2	
	Tubuaï	2		2		—	
	Moorea	3		2		1	
	Solomon	2		2		—	
	Vanuatu	5		2		4	
	Samoa	6		2		4	
	New Caledonia	4		2		3	
	Fidji	2		2		—	
	Futuna	1		—		1	
	Okinawa (Japan)	5		2		3	
	Philippines	1		1		—	
	Palau	1		1		—	
	Micronesia	2		2		—	
	Papua New Guinea	5		2		3	
	Reunion	2		2		2	
E. fornasini [Holotype BMNH 1852.9.13.179]	Mozambique	1		1		—	
E. klunzingerii	Mayotte	6	26	6	21	—	6
	Anjouan	2		—		2	
	Moheli	6		4		2	
	Madagascar	6		5		1	
	Reunion	4		4		—	
	Seychelles	2		2		1	
			T = 128		T = 99		T = 44

(Continues)

TABLE 1 (Continued)

Outgroup sequenced	Locality	*N*	*N* total	*COI*	*N* total	Partial mtDNA	*N* total
Belobranchus belobranchus	Philippines	1	1	1	1	—	—
Bunaka gyrinoides	Solomon	1	1	1	1	—	—
Outgroup from GenBank	**sequence ID**						
Eleotris oxycephala	KP713717						
Bostrychus sinensis	NC017880						

from Madagascar (MNHN 1984-0803). *Eleotris pellegrini* Maugé, 1984: syntypes from Madagascar (MNHN 1932-0108). *Eleotris aquadulcis* Allen & Coates, 1990: holotype from Papua New Guinea (WAM P.29608-006).

2.2 | Cephalic sensory papillae

Three rows are on the operculum: one transversal "*ot*" and two longitudinal (upper one "*os*," lower one "*oi*") (Figure

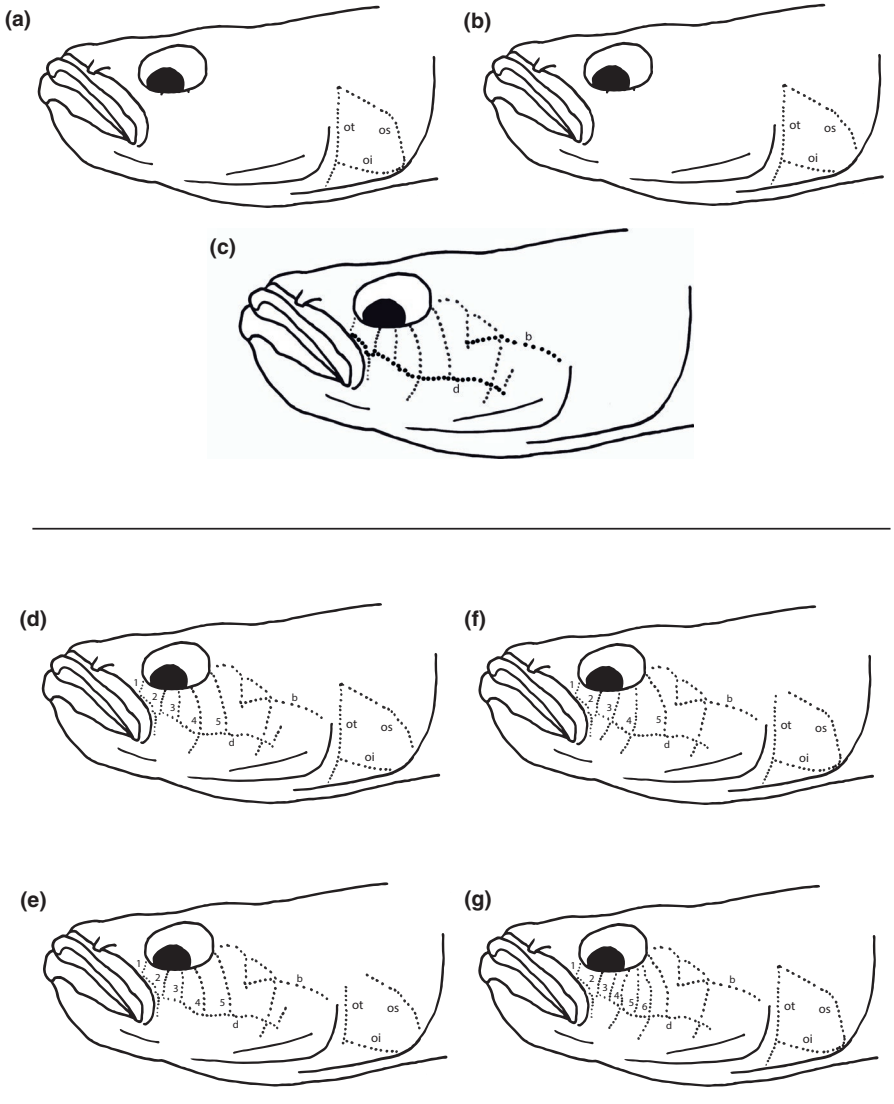

FIGURE 1 Schematic illustrations showing main cephalic free neuromast patterns. Opercular patterns (a: "closed"; b: "open"), two main rows under the eye (c: rows b and d) and cheek patterns (d: "2.4", e: "2", f: "2.3.4", g: "2.4.6")

1a,b). According to how these rows meet, two patterns are observed: when the rows "*os*" and "*oi*" meet, near the suboperculum, it is called "closed" (Figure 1a); when they do not meet, it is called "open" (Figure 1b).

Several rows are under the eye, two main horizontal ones noted *b* and *d* and several vertical ones noted from 1 to "n" (Figure 1c,d). The different patterns formed by these rows are distinguished by the number of vertical rows extending ventrally beyond their intersection with horizontal row *d*. For example, if the vertical lines 2, 4 and 6 intersect the horizontal line *d*, then we obtain the formula "2.4.6" for the pattern in question (Figure 1g). All the specimens studied, according to the work of Mennesson (2016), were sorted according to the arrangement of their cephalic sensory papillae rows, using the "open" or "closed" and "x.y.z" patterns (Table 2 and Figure 1d–g).

2.3 | DNA extraction and amplification

DNAs were extracted using Macherey & Nagel NucleoSpin® Tissue kits following the manufacturer's instructions on an Eppendorf EpMotion 5075, Qiagen DNeasy Blood & Tissue kit, or Promega Maxwell RSC Blood DNA kit.

2.3.1 | Partial cytochrome oxydase I gene

Ninety-nine specimens collected, including *E. fornasini* type, and 2 specimens used as outgroup were sequenced for cytochrome oxydase I gene (*COI*) gene. A mitochondrial fragment of the *COI* gene (585 bp) was amplified using the specific fish primers TelF1 and TelR1 (Dettai et al., 2011; Table 3). DNA amplification was performed by PCR in a final 20 µl volume containing 5% DMSO, 1 µl of BSA, 0.8 µl of dNTP 6.6 µM, 0.15 µl of Qiagen Taq DNA polymerase, using 2 µl of the buffer provided by the manufacturer, and 0.4 µl of each of the two primers at 10 p.m.; 1.2 µl of DNA extract was added. After denaturation for 2 min at 94°C, the PCR was run for 55 cycles of (25 s, 94°C; 25 s, 54°C; 55 s, 72°C) on a Bio-Rad C1000 Touch Thermal Cycler. Successful PCRs were selected on ethidium bromide-stained agarose gels. Sanger sequencing was performed in both directions by a commercial company (Eurofins; http://www.eurofins.fr) using the same primers.

TABLE 2 Arrangement of cephalic sensory papillae rows according to each species

Opercular pattern	Cheek pattern	*Eleotris* species
Closed	2.4.6	*E. fusca, E. klunzingerii, E. bosetoi*
	2.3.4	*E. melanosoma*
	2.4.5.6	*E. eigenmanni*
Open	2.4	*E. acanthopoma, E. mauritiana, E. sandwicensis, E. aquadulcis, E. pellegrini, E. vomerodentata*
	2	*E.oxycephala, E. balia*

2.3.2 | Partial mitochondrial genome (mtDNA)

Thirty-seven specimens were sequenced for the complete mitogenome using next-generation sequencing (NGS). Complete mitogenomes were obtained following the protocol established by Hinsinger et al. (2015) and using specific fish primers listed in Table 3. Hinsinger et al. (2015) developed a specific framework for the sequencing and multiplexing of mitogenomes on NGS platforms following 3 steps: (a) a universal long-range PCR-based amplification technique; (b) a two-level multiplexing approach and (c) a dedicated demultiplexing assembling script from an Ion Torrent sequencing platform. With this method, obtaining complete or almost complete mitogenome sequences are now easier and low cost. Moreover, having an extensive dataset for each specimen (i.e., 13 protein-coding genes, 22 tRNA genes, 2 rRNA genes and the control region; namely around 17,000 bp) allows (a) to easily compare the data obtained with those available in GenBank and (b) to have the best precision of the species genetic history by targeting the most variable genes.

Seven specimens were sequenced using shotgun-sequencing libraries with a KAPA HyperPlus kit, PCR-free (KAPA Biosystems). Shotgun libraries were then sequenced on either an Illumina MiSeq or HiSeq sequencers following manufacturer instructions.

We amplified the 37 mitogenomes with three overlapping fragments (primers used are in Table 3). A HotStart LongAmp® Taq DNA Polymerase (New England Biolabs) modified protocol was used. The three fragment amplifications were performed by PCR in a final 18 µl volume including 5X LongAmp Taq Reaction Buffer, 0.4 ng/µl Bovine Serum Albumin, 3.5% DMSO, 300 nM of each primer, 300 µM of dNTPs and 1 unit of LongAmp Taq polymerase. After an initial denaturation of 30 s at 94°C, the DNA was amplified through 45 cycles of 20 s at 94°C, 30 s at 62.5°C and 15 min at 65°C, with a terminal elongation for 15 min at 65°C (Hinsinger et al., 2015) on a Bio-Rad C1000 Touch Thermal Cycler. Successful PCRs were selected on ethidium bromide-stained agarose gels.

2.4 | DNA analysis

2.4.1 | Partial *COI* gene

Data processing and sequence assembly were done in Geneious 9.0.5 (http://www.geneious.com, Kearse et al., 2012). All the *COI* sequences were aligned with Muscle

TABLE 3 List of the primers used in this study for short and long PCRs

Genes	Primer name	Sequence (5'−3')	Publication
COI	Tel F1	TCGACTAATCAYAAAGAYATYGGCAC	Dettai et al. (2011)
COI	Tel R1	ACTTCTGGGTGNCCAAARAATCARAA	Dettai et al. (2011)
Complete mitogenome	12S-L1091R	AAACTGGGATTAGATACCCCACTAT	Kocher et al. (1989)
Complete mitogenome	MtH7061	GGGTTATGTGGCTGGCTTGAAAC	Hinsinger et al. (2015)
Complete mitogenome	MtL5231	TAGATGGGAAGGCTTCGATCCTACA	Hinsinger et al. (2015)
Complete mitogenome	MtH11944	CATAGCTTTTACTTGGATTTGCACCA	Hinsinger et al. (2015)
Complete mitogenome	MtL11910	CAGCTCATCCATTGGTCTTAGGAAC	Hinsinger et al. (2015)
Complete mitogenome	12S-H1478	TGACTGCAGAGGGTGACGGGCGGTGTGT	Hinsinger et al. (2015)

Alignment. A phylogenetic tree was performed using Bayesian inference (MrBayes v.3.2; Ronquist et al., 2012). Three models, corresponding to the three-codon positions, computed in PartitionFinder (Lanfear, Calcott, Ho, & Guindon, 2012) (1st position, SYM + I model; 2nd position, F81 model; 3rd position, HKY + G model) were run for 10 million generations, sampling every 200 generations with two independent runs to access convergence. Run convergence was checked using TRACER v.1.6.0 (Rambaut & Drummond, 2007). Trees were summarised using the 50% majority rule method after discarding the first 25% of the sample as burnin and visualised using FigTree v.1.4.2 (Rambaut, 2007). For the outgroup, we included a sequence of two other genera of Eleotridae, *Belobranchus belobranchus* and *Bunaka gyrinoides*.

2.4.2 | Partial mtDNA

The thirty-seven mitochondrial genomes reconstruction (except for *E. oxycephala* KP_713717, L. Zhong, X. Chen, M. Wang, W. Bia, D. Li, S. Tang, T. Zhang and Y. Shi, 2017; unpublished) was made using a starting reference, *Eleotris acanthopoma* mtDNA (Miya et al., 2003), available on MitoFish (Mitochondrial Genome Database of Fish; Iwasaki et al., 2013). The consensus of each mitogenome was primarily checked manually (assembly success, coverage assessment, comparison to available *COI* sequences for the same specimen, BLAST searches; Altschul et al., 1997) in Geneious 9.0.5 (Kearse et al., 2012). Then, the consensus sequence was annotated using MitoAnnotator (Iwasaki et al., 2013), and each gene was quality checked for coding sequences, stop codons and position of the SNPs. After checking the content and the order of each gene, mitogenomes were aligned with MAFFT 7.309 (implemented in Geneious).

Sequencing data from the seven shotgun libraries were assembled with the IDBA_UD assembler v.1.1.154 with different kmer lengths (60, 80, 100). Complete mitochondrial genomes were aligned using MAFFT v7.24455, and all positions with gaps were removed using trimAl56.

In the present study, we decided to use 12 protein-coding genes and not the complete mitogenome (10,115 vs. ≈ 16,500 bp) because the 22 tRNA genes, the 2 rRNA genes and the control region were not informative enough; percentages of divergence were under 3% while for protein-coding genes they were higher than 3% and several mitogenomes presented an incomplete tRNA-Asn ($N = 2$) and/or an incomplete ND4 gene ($N = 2$). However, we also performed an analysis in the complete mitogenome (without tRNA-Asn and ND4 gene) dataset to check whether the results were the same. A phylogenetic tree based on the twelve concatenated genes was performed using Bayesian inference (MrBayes v.3.2; Ronquist et al., 2012). The best-fitting models of evolution were computed in PartitionFinder (Lanfear et al., 2012). The analysis was undertaken using the three-codon positions for each gene as partition (Table 4) and was run for 10 million generations, sampling every 200 generations with two independent runs to access convergence. For each analysis, run convergence was

TABLE 4 Details of BIC models used for the three-codon positions for each gene

BIC Model	Gene_codon positions
GTR + G	ATP6_1, ND1_1, ND2_1, ND3_1, ND5_1, Cytb_1,
GTR + I	ATP6_2, ATP8_2, COII_2, ND1_2, ND2_2, ND3_2, ND4L_2, ND5_2, Cytb_2
GTR + I + G	ATP6_3, ATP8_3, COI_3, COII_1, COIII_3, ND1_3, ND2_3, ND3_3, ND4L_3, ND5_3, ND6_1, ND6_3, Cytb_3
SYM + I	ATP8_1, COI_1, COII_I, COIII_1, ND4L_1, ND6_2
F81 + I	COII_2, COI_2

checked using TRACER v.1.6.0 (Rambaut & Drummond, 2007). Trees were summarised using the 50% majority rule method after discarding the first 25% of the sample as burnin and visualised using FigTree v.1.4.2 (Rambaut, 2007). The percentage of differences between sequences and the number of bases, which are not identical, were calculated on Geneious 9.0.5. One species of another genus of Eleotridae, *Bostrychus sinensis*, was used as outgroup; this mitogenome was available on MitoFish (NC_017880).

3 | RESULTS

According to the work of Mennesson (2016) after type specimen examination and measurements, the morphological and meristic identification of the specimens indicated that seven species were represented (Table 1): *E. oxycephala* Temminck & Schlegel, 1845 (Japan & China), *E. sandwicensis* Vaillant & Sauvage, 1875 (Hawaii), *E. acanthopoma* Bleeker, 1853 (Pacific Ocean), *E. melanosoma* Bleeker, 1853 (Indo-Pacific), *E. bosetoi* Mennesson et al., 2016 (Solomon Islands), *E. fusca* (Bloch & Schneider, 1801) (Indo-Pacific) and *E. klunzingerii* Pfeffer, 1893 (Indian Ocean). As no types are available for *E. fusca* (Bloch & Schneider, 1801) and *E. mauritiana* Bennett, 1832, types of synonyms were also examined. At this step of the study, *E. mauritiana* (Indian Ocean) and *E. acanthopoma* (Pacific Ocean) are considered to be the same species.

Four of the five cephalic sensory patterns known in *Eleotris* species in the Indo-Pacific were represented in our samples: open "2" (Figure 1e), open "2.4" (Figure 1d), closed "2.4.6" (Figure 1g), closed "2.3.4" (Figure 1f). The fifth (closed "2.4.5.6") is only known for the lectotype and paralectotypes of *E. eigenmanni* Popta, 1921, which was not found in our samples.

3.1 | Phylogenetic reconstruction based on partial *COI* gene

A total of 585 bp of *COI* gene from 101 individuals were obtained and deposited in GenBank (Accession Numbers: MH497885-86; MH497891-95; MH497898-497903; MH497933-34; MH497936-37; MH497945-48; MH497979-80; MH498046-47; MH497979-80; MH498046-47; MH498086-87; MH498090; MH498099-100; MH498124; MH498136-37; MH498153-56; MH498167-68; MH498206; MH498220-21; MH498288-89; MH498351-56; MH498362; MH498392-93; MN045234-69). The Indo-Pacific *Eleotris* constitute a monophyletic group (*E. oxycephala* not included). The phylogeny has well-supported nodes (PP between 1 and 0.63; Figure 2) with two well-supported clades, I & II, with 13% of divergence representing 11 species. *Eleotris oxycephala* is outside the *Eleotris* clade (with 16.5% divergence).

Clade I is composed of two clearly identifiable species (5.5% of divergence), *E. klunzingerii* from the Indian ocean (I_1) and *E. fusca* from the Indian and Pacific oceans (I_2). Clade II is divided into two subclades A and B (14% of divergence). Subclade A is composed of two distinct groups: group A_1 consisting of *E. sandwicensis* and an "*E. acanthopoma"* subgroup including the specimens of *E. mauritiana*, and group A_2 formed by an unknown species called here *Eleotris* sp. Between *E. sandwicensis* and the "*E. acanthopoma"* subgroup, there is only 1.2% of divergence, while a divergence of 10% separates the A_1 group from the A_2 group. Subclade B consists of 3 branches, B_1 and B_2 which are in the subgroup called "*E. melanosoma* complex," and B_3. B_2 consists of two groups (6.6% of divergence): the first group B_2** is divided into two entities (5.2% of divergence) and presumably consists of the real *E. melanosoma* from Solomon Islands, Philippines and Vietnam (unpublished data), and a new species named here *E.* cf. *melanosoma* sp1 from Moorea (French Polynesia) and Okinawa (Japan). The second group B_2* is composed of only two individuals of a new species from the Indian Ocean (Mayotte) named here *E.* cf. *melanosoma* sp2. B_3 is consisted of *E. bosetoi* and differs from the B_2 by 10.5% of divergence. B_1 consisting of a new species referred to here as *E.* cf. *melanosoma* sp3, which diverges from B_3 and B_2 by 11% and 12%, respectively.

3.2 | Phylogenetic reconstruction based on partial mtDNA

A total of 41 complete and 3 partial mitogenomes (10,115 bp) were obtained, representing six species and one species complex, and were deposited in GenBank (Accession Numbers: MH367493-99; MH463444-50; MH479386-479400). After alignment of the 46 concatenated sequences, the maximum percentage of divergence between two sequences was 20.8% (between the outgroup *Bostrychus sinensis* and *E. acanthopoma*) with about 2,105 different nucleotides. The minimum percentage of divergence between two different species of *Eleotris* is 5.6% (*E. melanosoma* and *E.* cf. *melanosoma* sp1) with about 572 different nucleotides. To facilitate the reading, we kept the same letters (A, B, C) from the *COI* phylogeny to characterise the same clades.

The phylogenetic tree obtained by Bayesian Inference is basically divided into two well-supported clades, A and C, with 16% divergence (Posterior Probability, PP = 1) from the outgroups (Figure 3). The topology of this phylogeny is slightly different from the one obtained with the fragment of the partial *COI* gene; indeed, clade A is not anymore sister of the B one, and unfortunately, we cannot obtain mitogenomes for 2 species (*E.* cf. *melanosoma* sp2, and *E. sandwicensis*).

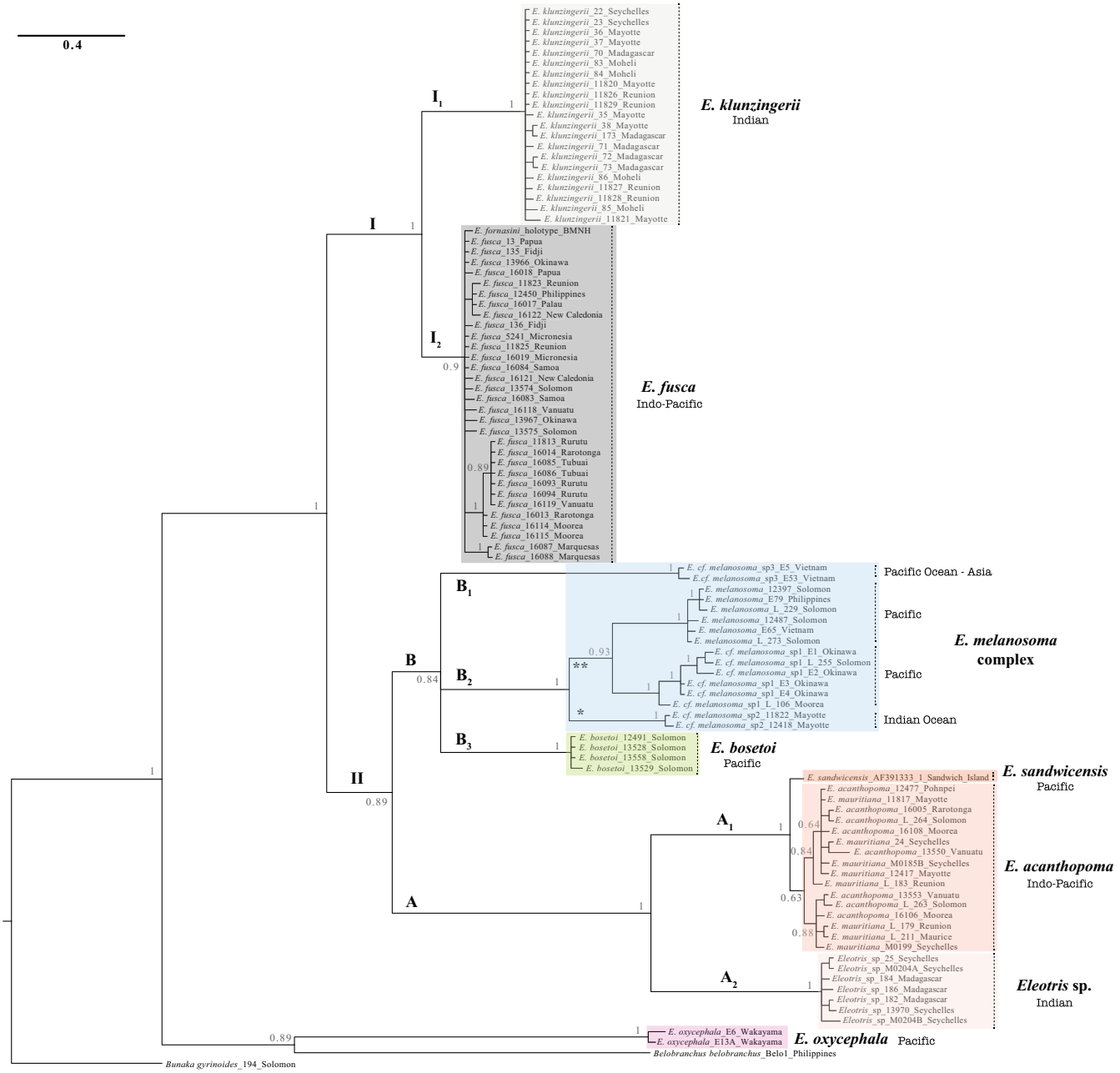

FIGURE 2 Bayesian tree of the *COI* gene (585 bp) for sequences specimens of *Eleotris*. Numbers on nodes represent posterior probabilities. Localities are indicated for each clade. In light grey: *E. klunzingerii*; grey: *E. fusca*; blue: *E. melanosoma* complex; green: *E. bosetoi*; peach: *E. sandwicensis*; light rose: *E. acanthopoma*; creme: *Eleotris* sp.; pink: *E. oxycephala*

Nevertheless, all the nodes are strongly supported (all PP equal to 1 except one at 0.86; Figure 3).

The first clade A is composed of two specimens belonging to two different species (11.2% of divergence), *E. acanthopoma* (A_1) and *Eleotris* sp. (A_2). The second clade C is composed of six species with two subclades I and B differing by 10.5% divergence. Subclade I consists of *E. klunzingerii* from the Indian Ocean (I_1) and *E. fusca* from the Indian and Pacific oceans (I_2) diverging by 6%. Subclade B has three branches (B_1, B_2, B_3) corresponding to *E.* cf. *melanosoma* sp3, *E. melanosoma—E.* cf. *melanosoma* sp1 and *E. bosetoi,* respectively. As we could not sequence the mitogenome of *E.* cf. *melanosoma* sp2, and *E. sandwicensis*, those species are absent from this tree. The divergence percentages between these three groups are similar to those obtained with the first phylogeny: B_1 differs from B_2 and B_3 by 12.3% and 11.3%, respectively; B_2 differs from B_3 by 10.3%, and the two groups of the B_2 branch (* and **) differ by 5.7% of divergence. All the species of the clade B are well-differentiated, and the relationships between the species are well-supported. As in the *COI* phylogeny, *E. oxycephala* is also outside the main *Eleotris* clade (16.4% of divergence).

3.3 | Morphology versus phylogeny

Morphologically, seven species were identified but eleven were found with the genetic analysis. This difference is mainly due to the fact the specimens' number of several new species is low not allowing us to have enough morphological data.

From the two phylogenies, we wanted to know if a link existed between the topology and the morphological criteria of cephalic sensory papillae. So, we superimposed the cephalic sensory papillae rows on both phylogenetic reconstructions, and only the one based on the partial mtDNA was congruent with cephalic sensory papillae pattern distribution (Figure 3). In this phylogeny, clade A presents the "open" pattern of the operculum sensory papillae, and the clade C is characterised by the "closed" one. The phylogeny based on the partial mtDNA thus reflects the morphology of the opercular papillae.

In contrast, our phylogeny seems not to reflect completely the type of infraocular sensory papillae as the "2.4.6" pattern is found in two different clades (I and B), but the "2.3.4" and "2.4" are specific to clade B and A, respectively.

4 | DISCUSSION

At the beginning of this study, we identified seven species of *Eleotris* distributed in the Indo-Pacific based on the morphological criteria of cephalic sensory papillae (Mennesson, 2016; Pezold & Cage, 2002) and previous studies (Mennesson et al., 2018, 2016; Mennesson & Keith, 2017). But we highlighted 11 species using DNA analysis (including four cryptic species). Although the two phylogenies presented well-supported clades, only the one based on the partial mtDNA (10,115 bp) reflected the morphology of opercular papillae. Indeed, the *COI* phylogeny was useful to detect the 11 species but 585 base pairs were not enough for having a high phylogeny resolution. From a taxonomic point of view, the four cryptic species are currently being studied by the authors.

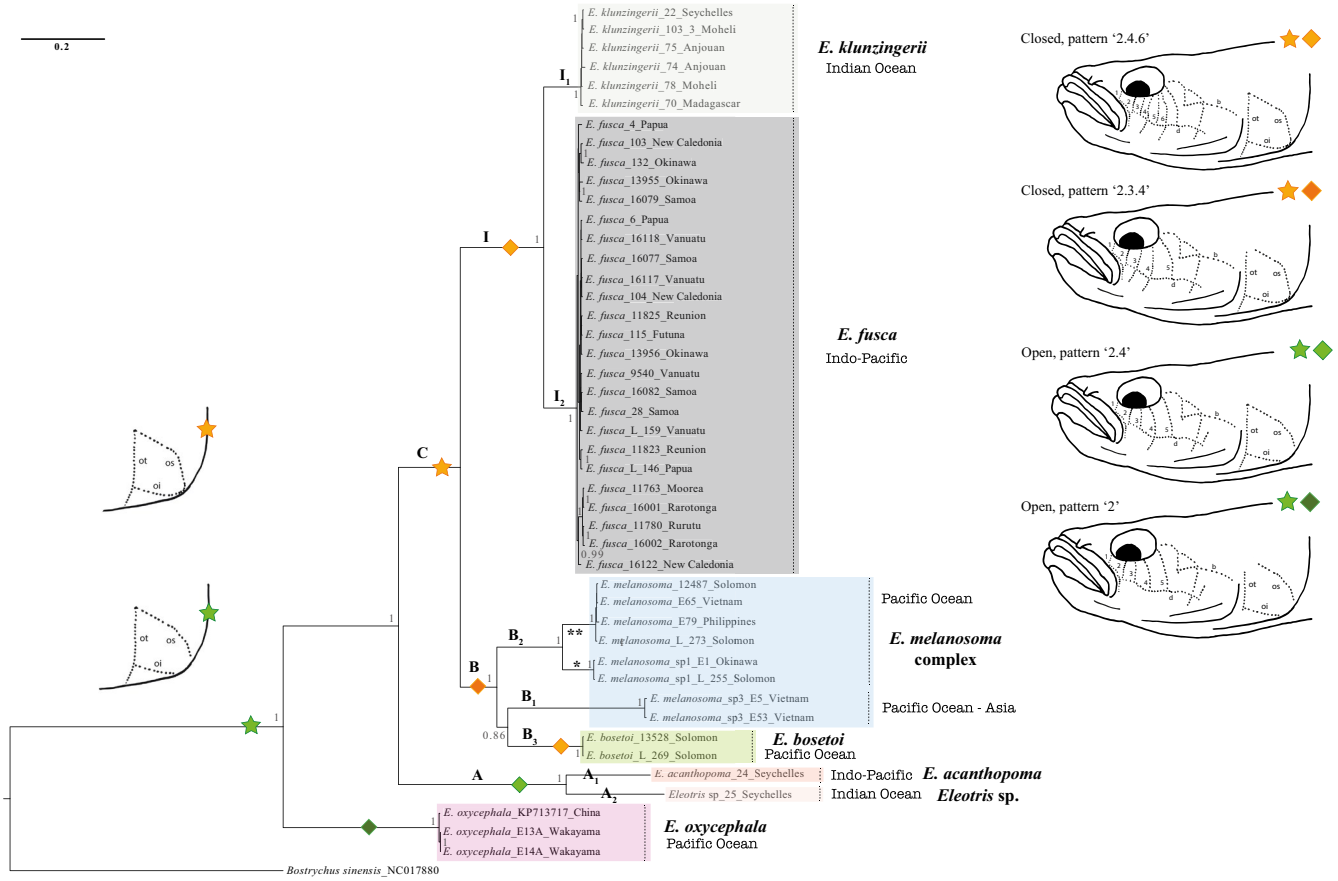

FIGURE 3 Arrangement of cephalic sensory papillae rows of each clade observed in the Bayesian tree of the partial mtDNA (10,240 bp). Numbers on nodes represent posterior probabilities. Localities are indicated for each clade. Each star corresponds to an opercular pattern (yellow: "closed"; green: "open"), and each diamond corresponds to a cheek patterns (yellow: "2.4.6"; orange: "2.3.4"; green: "2.4"; deep green "2"). In light grey: *E. klunzingerii*; grey: *E. fusca*; blue: *E. melanosoma* complex; green: *E. bosetoi*; light rose: *E. acanthopoma*; creme: *Eleotris* sp.; pink: *E. oxycephala*

4.1 | Clade A: Pattern "open; 2.4"

In clade A_1, from the *COI* tree (Figure 2), we found specimens identified as *E. mauritiana* (Indian Ocean) and those identified as *E. acanthopoma* (Pacific Ocean) grouped together (0.6% of divergence), which confirmed that they are the same species *that is E. acanthopoma* Bleeker, 1853 as assumed by Mennesson (2016). This latter species is thus a species with a large distribution (Indo-Pacific). A new species was highlighted called here *Eleotris* sp (clade A_2), which is morphologically close to *E. acanthopoma,* but separated by 10% of divergence. It is currently only known from the Seychelles islands and Madagascar. Although only 1.2% separates *E. acanthopoma* from *E. sandwicensis* (Hawaii), suggesting a recent divergence between these two species, Mennesson (2016) showed that these two species are valid as their morphologies are strongly distinct.

4.2 | Clade I: Pattern "closed; 2.4.6"

Clade I of both trees (Figures 2 and 3) contains the two sister species *E. fusca* and *E. klunzingerii.* The latter species was resurrected by Mennesson and Keith (2017) and Mennesson et al. (2018). These two species are morphologically close, but genetically distinct (6% of divergence). The type of *E. fornasini,* here successfully sequenced in *COI,* is in the *E. fusca* clade and is regarded as a synonym of this species.

4.3 | Clade B: Patterns "closed; 2.4.6" & "closed; 2.3.4"

Clade B was comprised of specimens believed to be the wide-ranging Indo-Pacific species *E. melanosoma* with all individuals sharing the same pattern "closed; 2.3.4." However, percentages of divergence (5.7%–12.3%) and node resolution (PP = 1) indicated the presence of 4 species including three cryptic forms: *E.* cf. *melanosoma* sp1, *E.* cf. *melanosoma* sp2 and *E.* cf. *melanosoma* sp3. Consequently, *E. melanosoma* appears to be restricted to the Pacific Ocean in sympatry with two other species: *E.* cf. *melanosoma* sp1 and *E.* cf. *melanosoma* sp3. *E.* cf. *melanosoma* sp2 is limited to the Indian Ocean.

Although *E. bosetoi* has the same infraocular sensory papillae pattern ("closed; 2.4.6") as *E. fusca* and *E. klunzingerii* (Clade I), it belongs to the clade B whatever the tree obtained.

Our work thus highlights, in a completely new way, that the mtDNA phylogeny of the *Eleotris* reflects the evolution of their opercular papillae (open pattern: clade A; closed pattern: clade C) (Figure 3). Nevertheless, our phylogeny seems not to reflect completely the type of infraocular sensory papillae as one pattern is found in the two clades A and C, but two others are clade-specific. Even if we do not currently know what are the consequences of free neuromast pattern variations, particularly in terms of life traits and ecology, there is no geographic pattern within clades according to the arrangement of sensory papillae.

The lateral line system of fish is made of a series of mechanoreceptors *that is* neuromasts on the head, trunk and tail. The first neuromasts appear in embryos under the membrane and lateral line nerves induct their formation. Almost immediately after the appearance of the first neuromasts, the lateral line becomes active and functional (Kasumyan, 2003). Free neuromasts (i.e., located freely at the surface of the body) are known to be useful for obtaining information about the water current and for the perception of oscillations caused by large movable objects (Hofer, 1908). Many parts of the individual behaviour are linked to the lateral line such as feeding, defence, schooling, reproduction and migration, allowing fish to orient in darkness and perform rheoraction (i.e., ability to perceive linear velocity variations of current). The ability of fish to respond to oscillations caused by other moving organisms allows them to determine the presence of the prey, detect its location with high precision and to strike its target.

The number and also the distribution of free neuromasts in *Eleotris* might be linked to aspects of the lifestyle such as the feeding habits (e.g., carnivorous), hunting strategy (e.g., sit-and-wait predator) or preferred habitat (Kasumyan, 2003). So, it will be very useful to study the life traits of the main species to know if there is a correlation between the life cycle or the habitat used and the cephalic sensory pattern. For example, is there any link between the preferred habitat (estuaries, lower course or middle course of river) and the sensory pattern of a species, as the habitat could induce differences in terms of hunting or feeding habits? As we found cryptic species in *Eleotris*, knowing the specific life traits of each species will be challenged.

Miller (1998) elaborated a phylogeny based on morphology and subdivided *Eleotris* into clusters of nominal species based upon cephalic neuromast patterns. Pezold and Cage (2002) stated that, although there is heuristic value in his approach, cephalic free neuromast patterns must be used with caution in any phylogenetic reconstruction. Indeed, in their study of eastern Pacific and western Atlantic *Eleotris*, the suborbital row patterns sometimes vary intraspecifically, and that variation was significant. Variation among their species also existed for the presence or absence of the *ot'* row that Miller regarded as a synapomorphy for *Eleotris.* They concluded that before an unequivocal phylogeny of intrageneric relationships can be developed, more polarised characters are needed, and this demands a better understanding of eleotrid relationships. For them, another major problem confronting any attempt at phylogenetic reconstructions of intrageneric *Eleotris* relationships was that morphological variation within and among Indo-Pacific species required attention. Indeed, at the beginning of the twenty-first century only

Akihito's work (1967) was known on the subject. That was the aim of the study of Mennesson (2016) and unlike Pezold and Cage (2002) she did not observe any variations of the free neuromast pattern within Indo-Pacific species. Our phylogeny is consistent with the hypothesis of Miller (1998) that the "closed" pattern on the opercular seems to be derived.

Pezold and Cage (2002) suggested instead of any active genetic exchange across the Atlantic (their study) that *Eleotris* was simply morphologically conservative. Similar morphotypes to those they studied in the western hemisphere and the Eastern Atlantic pop up in other tropical estuaries and insular streams, albeit ever so slightly different. Since 2016, two new species of *Eleotris* in the Western Atlantic were discovered (Guimarães-Costa et al., 2016), but unfortunately no study of the free neuromasts was done. Present circumglobal distributions of *Eleotris* suggest that several basic lines were separated a long time ago.

The place of *Eleotris oxycephala* (potential 3rd group) in our phylogeny remains to be discussed as indicated by the results of some other phylogenies published on Eleotridae and Gobioidei. Indeed, in 2012, Agorreta and Rüber tested the robustness of several Gobioidei phylogenies published in the early 20th century using new techniques of parsimonious molecular reconstructions. Among these phylogenies, two of them are interesting—one based on the Cytochrome *b* gene (1,140 bp) using data from Akihito et al. (2000) and one based on 12*S* rRNA gene (905 bp) using data from Wang, Tsai, Dean, and Lee (2001)—as they include the three main species of *Eleotris* in the Indo-Pacific (i.e., *E. fusca, E. melanosoma* and *E. acanthopoma*) and a sequence of *E. oxycephala*. Like in our *COI* phylogeny, the place of *E. oxycephala* is unclear within the *Eleotris* genus, which might suggests i—that the species is possibly not part of this genus or ii—there is a possible long branch attraction that affects the base of these phylogenies. Nevertheless, the phylogeny of Eleotridae carried out on the gene Cytochrome *b* (1,265 bp) by Wei, Jin, and Xu (2013) showed the presence of *E. oxycephala* at the base of the origin of the genus as we noticed in our partial mtDNA phylogeny (10,115 bp). According to our study, *E. oxycephala* presents an "open" pattern so if its correct place is at the base of the genus *Eleotris*, this might suggest that the common ancestor of the *Eleotris* could have such pattern.

5 | CONCLUSION

In this paper, the two phylogenetic reconstructions based on the mitochondrial genome allowed the molecular distinction of 11 species of *Eleotris* (including 4 cryptic species), and it also allowed the resolution of interspecific relationships. Hence, two well-supported clades were recovered with a strong correlation to the evolution of the opercular papillae. The morphology of these cephalic sensory papillae is of particular importance in this predatory genus as it is generally correlated in fish to predation and feeding. As a perspective to this work, one of the aims would be to include, in a new phylogeny, a greater number of specimens belonging to *E. oxycephala,* of the cryptic species, and if possible to include also the species *E. eigenmanni*, which has the 5th papillae pattern ("closed; 2.4.5.6"), but which is actually only known by types. This would allow us to reinforce the results obtained. But, the study of the various mechanisms leading to the slight differences in sensory patterns between the different species in terms of food habits and habitat preferences, and enabling them to co-occur, remains to be done. Thus, the study of the life traits of the main species of Indo-Pacific *Eleotris* is needed.

ACKNOWLEDGEMENTS

The authors thank David Boseto, Brendan Ebner, Philippe Gerbeaux, Gérard Marquet for their help collecting specimens in the Solomon Islands. The study was made possible by a grant given to the French Ichthyologic Society in the context of the "Critical Ecosystem Partnership Fund (CEPF)" (Melanesia hotspot). The Critical Ecosystem Partnership Fund is a joint initiative of l'Agence Française de Développement, Conservation International, the Global Environment Facility, the Government of Japan, the MacArthur Foundation and the World Bank. A fundamental goal is to ensure civil society is engaged in biodiversity conservation. We would like to acknowledge the customary landowners and tribes from Choiseul, Kolobangara and Vella Lavella, KIBCA and ESSI, and the Solomon Islands Government for the support and facilitation of the legal process that have allowed the expedition team to conduct the scientific research. Thanks to Clementine Flouhr, Cendrine Meresse for their help collecting specimens in New Caledonia. The work was supported North and South Province of New Caledonia. We would like to thank Jean–Jérôme Cassan (North Province) and Damien Grima (South Province) for providing us the research permit. Thanks to Brian Lynch, Magalie Castelin, Laura Taillebois and Philippe Gerbeaux for their help collecting specimens in Palau and Micronesia. We would like to thank the Ministry of Natural Resources, Environment, and Tourism Koror, Republic of Palau, the Bureau of Marine Resources, and the Bureau of Agriculture (BOAGRI), for their help with processing the research permits. Thanks to the Conservation Society of Pohnpei and the Office of Fisheries and Aquaculture. Thanks to the Direction de l'agriculture et de la forêt and ARDA (Association Réunionaise de Développement de l'Aquaculture) for their help collecting specimens in Mayotte, Réunion and Mauritius. Thanks to Y. Ibrahin (CNDRS) and A. Abdou

for specimens from Comoros. For the Seychelles, we would like to thank the UNDP and particularly E. Henriette and B. Santerre. Thanks to the DIAMSOI team (research financed by the Institut Français de la Biodiversité (IFB)) for their help collecting specimens in Madagascar. We are grateful to Joe Aride from Madagascar National Parcs (MNP-ANGAP). Thanks to the Office of the Prime Minister of Rarotonga for the research permit in the Cook Islands. For Samoa thanks to the Samoan Ministry of Natural Resources Environment and Meteorology (MNRE), the International Union for Conservation of Nature (IUCN) and J. Atherton. For French Polynesia, we thank Jean-Yves Meyer and the Marquesas Islands mayors. For Vanuatu, we thank the Environment Unit of Vanuatu, with special thanks to Donna Kalfatak. Thanks to Katsumi Tsukamoto, Shun Watanabe and Midori Iida for specimens from Japan. For Philippines, we thank Okinawa Institute of Science and Technology Graduate University (OIST) and Western Philippines University (WPU) and more especially Herminie P. Palla (WPU). We are grateful to the Palawan Council for Sustainable Development, Puerto Princesa City and Barangay Binduyan for their help with processing the research permits. Specimens from Vietnam were collected under a Memorandum of Agreement for joint research between OIST and Hanoi National University of Education (HNUE). We especially thank Hau Duc Tran (HNUE) for this collaboration. We are grateful to the Ministry of Natural Resources and Environment and Da Nang City for providing a research permit. For Papua New Guinea thanks to P. Amick (NBRI) and the Conservation and Environment Protection Authority (CEPA). For the loan of specimens, we thank: D. Catania (CAS), R. de Ruiter (RMNH), S. Dorow, H. Zetzsche, T.J. Alpermann and F. Krupp (SMF), S. Morrison and G.R. Allen (WAM), R. Vonk and H. Praagman (ZMA), R. Hadiaty (MZB), S. Merker (SMNS), I. Eidus (ZMH), T. Heath and J. Maclaine (BMNH), L. Parenti, J. Williams, L. Palmer and S. Raredon (USNM), P. Pruvost, R. Causse, Z. Gabsi, C. Ferrara, M. Hautecœur (MNHN). Thanks to the Service de Systématique Moléculaire of the MNHN and its staff for (UMS2700 MNHN/CNRS) for granting access to its technical platform and allowing us to perform the molecular work and Ryo Koyanagi (OIST) for DNA sequencing at OIST and Chuya Shinzato (University of Tokyo) for assembling the sequences. This work was supported by the National Museum of Natural History of Paris, the AIMARA Association, the French Ichthyological Society and JSPS KAKENHI Grant Number 16K07492.

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How to cite this article: Mennesson MI, Maeda K, Keith P. Evolutionary aspects of cephalic sensory papillae of the Indo-Pacific species of *Eleotris* (Teleostei: Eleotridae). *Zool Scr*. 2019;00:1–13. https://doi.org/10.1111/zsc.12366