

Eleotris (Teleostei: Eleotridae) of the Indian Ocean: an overview with the description of three new species

by

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Submitted: 7 Jul. 2020
Accepted: 20 Aug. 2020
Editor: R. Causse

Abstract. – Recent research studied the complexity of the taxonomy of the genus *Eleotris* (Teleostei: Eleotridae) highlighting the presence of cryptic species in the Indo-Pacific area. *Eleotris* species are one of the most common fish in lower and medium parts of insular freshwater streams. Here we studied specimens from several localities in the Indian Ocean and we described three new species (*Eleotris diamsoi*, *E. sahanaensis*, and *E. valadei*), and we redescribed *E. pellegrini* Maugé 1984, *E. vomerodentata* Maugé, 1984 and *E. soaresi* Playfair, 1867. A key for *Eleotris* species from West Indian Ocean is provided.

Résumé. – *Eleotris* (Teleostei : Eleotridae) de l’océan Indien : bilan et description de trois espèces nouvelles.

Des recherches récentes ont souligné la complexité de la taxonomie du genre *Eleotris* (Teleostei : Eleotridae) mettant en évidence la présence d’espèces cryptiques dans la zone Indo-Pacifique. Les *Eleotris* sont des poissons communs dans les parties basses et moyennes des cours d’eau insulaires. Nous avons étudié ici des spécimens de plusieurs localités de l’océan Indien et nous décrivons trois nouvelles espèces (*Eleotris diamsoi*, *E. sahanaensis* et *E. valadei*), et nous redécrivons *E. pellegrini* Maugé 1984, *E. vomerodentata* Maugé, 1984 et *E. soaresi* Playfair, 1867. Une clé pour les espèces d’*Eleotris* de l’océan Indien occidental est fournie.

Key words

Eleotris
Cryptic species
Indian Ocean
Madagascar
Seychelles
Reunion Island
Comoros

INTRODUCTION

Among amphidromous fishes, the genus *Eleotris* (Teleostei: Eleotridae) is one of the most common in Indo-Pacific, in lower and medium parts of insular freshwater streams (Mennesson *et al.*, 2015, 2016, 2018). It is a sit-and-wait predator (Keith *et al.*, 2006) characterized by a distinctive eleotrid morphology – moderately blunt large head, torpedo-like body shape, broad rounded caudal fin and prominent lower jaw. It is well known that field identification of *Eleotris* species is difficult due to the lack of meristic characters without overlap and because all the species are generally brown and look alike (Mennesson *et al.*, 2019). Several authors found cephalic free neuromast patterns and differences in squamation to be the most useful characters in separating species (Akihito, 1967; Miller, 1988; Pezold and Cage, 2002); this was confirmed by Mennesson (2016), Mennesson *et al.* (2016) and Mennesson and Keith (2017). Recently, in their phylogeny of this genus in the Indo-Pacific area, Mennesson *et al.* (2019) showed that the presence and disposition of cephalic sensory papillae rows on the operculum and under the eyes are diagnostic characters. They dis-

tinguished five different patterns of row arrangement for the species (patterns ‘2’, ‘2.4’, ‘2.3.4’, ‘2.4.6’, and ‘2.4.5.6’), including the 15 presumed valid species (Pattern ‘2’: *Eleotris oxycephala* Temminck & Schlegel, 1845; *Eleotris balia* Jordan & Seale, 1905. Pattern ‘2.4’: *Eleotris acanthopoma* Bleeker, 1853; *Eleotris sandwicensis* Vaillant & Sauvage, 1875; *Eleotris vomerodentata* Maugé, 1984; *Eleotris pellegrini* Maugé, 1984; *Eleotris aquadulcis* Allen & Coates, 1990. Pattern ‘2.3.4’: *Eleotris melanosoma* Bleeker, 1853; *Eleotris macrolepis* (Bleeker, 1875); *Eleotris soaresi* Playfair, 1867. Pattern ‘2.4.6’: *Eleotris fusca* (Bloch & Schneider, 1801); *Eleotris klunzingerii* Pfeffer, 1893; *Eleotris macrocephala* (Bleeker, 1857); *Eleotris bosetoi* Mennesson, Keith, Ebner & Gerbeaux, 2016. Pattern ‘2.4.5.6’: *Eleotris eigenmanni* Popta, 1921; see methods for the pattern of the cephalic sensory papillae rows). In this study, they also highlighted the presence of several cryptic species distributed in Indian Ocean and they demonstrated that the *Eleotris* phylogeny reflects the morphology of the opercular papillae.

The aim of this paper is to review the *Eleotris* specimens found in Indian Ocean islands, using, when possible, genetic and morphometric approaches.

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MATERIALS AND METHODS

Sampling

The fish used for the study were collected from Indian island freshwater streams. In the field, individuals were sampled using a DEKA 3000 electrofishing system (Gerätebau, Marsberg, Germany). Following annex IV of the directive 2010/63/EU, fish were either euthanized using an overdose of clove oil (10%), or a piece of fin was taken while the fish was anaesthetised. In the case of anaesthetization, the fish was then awakened in clear water before it was released. Entire fish or fin clips were stored and preserved in 95% ethanol for molecular analysis. Sixty-five *Eleotris* specimens were used. Species, specimens and localities sampled are listed in table I.

Collected 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; ZMH: Zoological Museum Hamburg; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC).

The type specimens of *Eleotris* species examined (45) are listed below:

Pattern '2': *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).

Pattern '2.4': *Eleotris acanthopoma* Bleeker, 1853: holotype from Sumatra, Indonesia (RMNH 25934) [synonym: *Eleotris mauritiana* Bennett, 1832: Syntypes? BMNH from West Indian Ocean (1855.12.26.562, 2016.6.6.2)].

Eleotris sandwicensis Vaillant & Sauvage, 1875: syntypes from Hawaiian Islands (MNHN A-2624, 8045, 8915, 9011). *Eleotris vomerodontata* Maugé, 1984: holotype from Madagascar (MNHN 1984-0803). *Eleotris pellegrini* Maugé, 1984: syntypes from Madagascar (MNHN 1932-0108). *Eleotris aquadulcis* Allen & Coates, 1990: paratypes from Papua New Guinea (WAM P.29608-002).

Pattern '2.3.4': *Eleotris melanosoma* Bleeker, 1853: 2 syntypes from Wahai, Ceram (not Sumatra; probably a miswriting, indeed Bleeker's paper 'Nieuwe bijdrage tot de kennis der ichthijologische fauna van Ceram' is based mainly on fish collection done in Wahai Ceram), Indonesia (in RMNH 4815) [synonyms: *Culius insulindicus* Bleeker, 1875: syntypes from Sumatra, Indonesia (RMNH 4804). *Eleotris pseudacanthopomus* Bleeker, 1853: holotype from Western Sumatra, Indonesia (SMNS 10595), not synonym of *E. fusca*

as stated by Fricke *et al.* (2020). *Eleotris melanura* Bleeker, 1849: holotype from southern Java, Indonesia (in RMNH 5182); not synonym of *E. fusca* as stated by Fricke *et al.* (2020)].

Eleotris macrolepis (Bleeker, 1875): syntypes from Ambon, Indonesia (RMNH 4759) [not synonym of *E. melanosoma* as stated by Fricke *et al.* (2020)]. *Eleotris soaresi* Playfair, 1867: syntypes from Mozambique, Africa (BMNH 1865.3.18.26-27).

Pattern '2.4.6': *Eleotris fusca* (Bloch & Schneider, 1801): no type known [Synonyms: *Eleotris nigra* Quoy & Gaimard, 1824: 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 brachyurus* Bleeker 1849: syntype from Patjitan, southern Java, Indonesia (RMNH 5182)].

Eleotris klunzingerii Pfeffer, 1893: holotype from Zanzibar, Africa (ZMH-H412). *Eleotris macrocephala* (Bleeker, 1857): true holotype from Buru, Indonesia is RMNH 25935 and not RMNH 4757. *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).

Pattern '2.4.5.6': *Eleotris eigenmanni* Popta, 1921: syntypes from Sunda Islands, Indonesia (RMNH 10708 (1) not cited by Fricke *et al.* (2020); SMF 6594 (1) and SMF 6595-99 (5)) [not synonym of *E. fusca* as stated by Fricke *et al.* (2020)].

Morphometrics

Methods follow Mennesson *et al.* (2016). Specimens were measured with a dial calliper to the nearest tenth of a millimetre. All counts were taken from the right side. The size is given as standard length (SL).

Scale and fin ray counts are reported as: A, anal fin elements (includes flexible spine and segmented rays); D, dorsal fins (D1, first dorsal fin spines; D2, second dorsal fin elements); P, pectoral fin rays; C, caudal fin rays (only branched rays are reported); LS, scales in lateral series counted from upper pectoral fin base, or anteriormost scale along lateral midline, to central hypural base; PD, predorsal midline scales counted from scale directly anterior to first dorsal fin insertion to the anteriormost scale; TRB, transverse series backward, refers to scales counted from the first scale anterior to second dorsal fin origin, in a diagonal manner, posteriorly and ventrally to the anal fin base or ventralmost scale; TRF, transverse series forward, refers to scales counted from the first scale anterior to second dorsal fin origin, in a diagonal manner, anteriorly and ventrally to the centre of abdomen

Table I. – Species, specimens and localities sampled.

MNHN number	Tag number	Species	Archipelago	Island	River	Date	Collectors	n° COI GenBank	COI 584 bp	COI 79 bp
2006-0617	M-0617A	<i>E. acanthopoma</i>	Comoros Is.	Moheli	Mdjawaché	31/10/05	Keith <i>et al.</i>			
2006-0617	M-0617B	<i>E. acanthopoma</i>	Comoros Is.	Moheli	Mdjawaché	31/10/05	Keith <i>et al.</i>	MIN045244	x	x
2006-0617	M-0617C	<i>E. acanthopoma</i>	Comoros Is.	Moheli	Mdjawaché	31/10/05	Keith <i>et al.</i>			
2020-0029	12426	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Kwale	22/04/09	Feutry <i>et al.</i>	MIN045236	x	x
2020-0030	12417	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	–	April-09	Feutry <i>et al.</i>			
2020-0031	13951	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>			
2020-0032	13952	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>			
2020-0033	13953	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>			
2020-0034	13954	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>			
2020-0035	14519	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Coconi	06/08/19	Valade <i>et al.</i>			
2020-0036	14520	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Coconi	06/08/19	Valade <i>et al.</i>			
2020-0037	14521	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Coconi	06/08/19	Valade <i>et al.</i>			
2020-0038	14562	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ourovéni	06/08/19	Valade <i>et al.</i>			
2020-0039	14563	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ourovéni	06/08/19	Valade <i>et al.</i>			
2020-0040	14564	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Longoni	07/08/19	Valade <i>et al.</i>			
2020-0041	14564	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Longoni	07/08/19	Valade <i>et al.</i>			
2020-0041	11817	<i>E. acanthopoma</i>	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>	MIN045235	x	x
2007-0185	M-0185A	<i>E. acanthopoma</i>	Seychelles Is.	Mahe	–	24/11/04	Accouche <i>et al.</i>			
2007-0185	M-0185B	<i>E. acanthopoma</i>	Seychelles Is.	Mahe	–	24/11/04	Accouche <i>et al.</i>			
2007-0199	M-0199	<i>E. acanthopoma</i>	Seychelles Is.	Mahe	Anse aux poules bleues	14/10/03	Keith <i>et al.</i>	MIN045245	x	x
2007-0205	14509 (1 of 5)	<i>E. acanthopoma</i>	Seychelles Is.	Praslin	Fond B'Offay	10/10/03	Keith <i>et al.</i>		x	x
2020-0042	13749	<i>E. acanthopoma</i>	Seychelles Is.	Praslin	Nouvelle-Découverte	09/10/03	Keith <i>et al.</i>		x	x
2020-0079 extracted from 2007-0200	C	<i>E. acanthopoma</i>	Seychelles Is.	Mahe	–	22/11/04	Accouche <i>et al.</i>			
MNHN 2007-0204	M-0204A	<i>E. pellegrini</i>	Seychelles Is.	Mahe	Grande Anse	20/11/04	Accouche <i>et al.</i>	MIN045267	x	x
MNHN 2007-0204	M-0204B	<i>E. pellegrini</i>	Seychelles Is.	Mahe	Grande Anse	20/11/04	Accouche <i>et al.</i>	MIN045269	x	x
2020-0043	13970	<i>E. pellegrini</i>	Seychelles Is.	Silhouette	Anse Mondon	20/11/04	Accouche <i>et al.</i>	MIN045268	x	x
2020-0044	25	<i>E. pellegrini</i>	Seychelles Is.	Mahe	Bel ombre	24/11/12	Keith & Henriette	MIN045266	x	x
2007-0200	A	<i>E. pellegrini</i>	Seychelles Is.	Mahe	–	22/11/04	Accouche <i>et al.</i>			
2007-0200	B	<i>E. pellegrini</i>	Seychelles Is.	Mahe	–	22/11/04	Accouche <i>et al.</i>			
2020-0045	182	<i>E. pellegrini</i>	Madagascar	Madagascar	–	07/07/08	Diamsoi	MIN045265	x	x
2020-0046	184	<i>E. pellegrini</i>	Madagascar	Madagascar	–	07/07/08	Diamsoi	MIN045263	x	x
2020-0047	185	<i>E. pellegrini</i>	Madagascar	Madagascar	–	07/07/08	Diamsoi			
2020-0048	186	<i>E. pellegrini</i>	Madagascar	Madagascar	–	07/07/08	Diamsoi	MIN045264	x	x
2020-0049	7247	<i>E. pellegrini</i>	Madagascar	Madagascar	Andrepona	04/07/08	Diamsoi			
2020-0050	7246	<i>E. pellegrini</i>	Madagascar	Madagascar	Andrepona	04/07/08	Diamsoi			
2020-0051	7248	<i>E. pellegrini</i>	Madagascar	Madagascar	Andrepona	04/07/08	Diamsoi			
2020-0052	13015	<i>E. pellegrini</i>	Madagascar	Madagascar	Ambanizana	May-2010	Diamsoi			
2020-0053	13007	<i>E. pellegrini</i>	Madagascar	Madagascar	Farambana	July-2008	Diamsoi			
2020-0054	12947	<i>E. pellegrini</i>	Madagascar	Madagascar	Sahana	07/07/08	Diamsoi			
2020-0055	13001	<i>E. pellegrini</i>	Madagascar	Madagascar	Farambana	July-2008	Diamsoi			

Table I. Continued.

MNHN number	Tag number	Species	Archipelago	Island	River	Date	Collectors	n° COI GenBank	COI 584 bp	COI 79 bp
MNHN 1962-0172	3	<i>E. pellegrini</i>	Madagascar	Madagascar	Lampahana	-	Kiener			
MNHN 1962-0172	4	<i>E. pellegrini</i>	Madagascar	Madagascar	Lampahana	-	Kiener			
MNHN 1962-0172	6	<i>E. pellegrini</i>	Madagascar	Madagascar	Lampahana	-	Kiener			
2020-0056	12728	<i>E. pellegrini</i>	Seychelles Is.	Praslin	Fond B' Offray	22/02/20	Keith, Mennesson			
2020-0057	12730	<i>E. pellegrini</i>	Seychelles Is.	Praslin	Fond B' Offray	22/02/20	Keith, Mennesson			
2020-0058	12593	<i>E. pellegrini</i>	Seychelles Is.	Mahe	Grand St. Louis	15/02/20	Keith, Mennesson			
2020-0077	7278	<i>E. salhanaensis</i> n. sp.	Madagascar	Madagascar	Andrepona	04/07/08	Diamsoi		x	x
2020-0078	13003	<i>E. salhanaensis</i> n. sp.	Madagascar	Madagascar	Sahana	July-2008	Diamsoi		x	x
2020-0059	12418	<i>E. valadei</i> n. sp.	Comoros Is.	Mayotte	MtChangachahi	12/12/03	Marquet <i>et al.</i>		x	x
2020-0060	12950	<i>E. valadei</i> n. sp.	Madagascar	Madagascar	Ambodiforaha	July-2008	Diamsoi		x	x
2020-0061	11818	<i>E. valadei</i> n. sp.	Comoros Is.	Mayotte	Ouroveni	06/09/07	Marquet <i>et al.</i>			x
2020-0062	11822	<i>E. valadei</i> n. sp.	Comoros Is.	Mayotte	Ouroveni aval	20/04/09	Feutry <i>et al.</i>		x	x
2020-0063	14561	<i>E. valadei</i> n. sp.	Comoros Is.	Mayotte	Ouroveni	06/08/19	Valade <i>et al.</i>		x	x
2020-0064	12409	<i>E. valadei</i> n. sp.	Mascarene Is.	Reunion	(ARDA)	Dec.-2007	Zimmermann <i>et al.</i>			
2020-0065	12584	<i>E. valadei</i> n. sp.	Seychelles Is.	Praslin	Nouvelle-Découverte	21/01/20	Keith, Mennesson		x	x
2020-0066	183	<i>E. diamsoi</i> n. sp.	Madagascar	Madagascar	Sahana	07/07/08	Diamsoi		x	x
2020-0067	13016	<i>E. diamsoi</i> n. sp.	Madagascar	Madagascar	Ankazofotsy	May-2010	Diamsoi		x	x
2020-0068	13004	<i>E. diamsoi</i> n. sp.	Madagascar	Madagascar	Sahana	07/07/08	Diamsoi			x
MNHN 2016-0030	12397	<i>E. melanoxoma</i>	Solomon Is.	Kolobangara	Vage	10/11/15	Keith <i>et al.</i>		x	x
MNHN 2016-0031	12487	<i>E. melanoxoma</i>	Solomon Is.	Kolobangara	Vanga	18/11/15	Keith <i>et al.</i>		x	x
MNHN 2016-0032	L-229	<i>E. melanoxoma</i>	Solomon Is.	Kolobangara	Zamba	10/11/15	Keith <i>et al.</i>		x	x
MNHN 2016-0091	11827	<i>E. klunzingerii</i>	Mascarene Is.	Reunion	Saint Jean	24/03/07	Arda	MH498154	x	x
MNHN 2016-0091	11828	<i>E. klunzingerii</i>	Mascarene Is.	Reunion	Saint Jean	24/03/07	Arda	MH498155	x	x
2020-0074	22	<i>E. klunzingerii</i>	Seychelles Is.	Silhouette	Lo Glacis	29/11/12	Keith, Henriette	MH498353	x	x
2020-0075	66	<i>E. fusca</i>	Comoros Is.	Mayotte	-	Nov.-2003	Marquet <i>et al.</i>	MH497935	x	x
2020-0076	11825	<i>E. fusca</i>	Mascarene Is.	Reunion	Saint Jean	24/03/07	Arda	MH498168	x	x

65 specimens
8 species

or ventralmost scale; ZZ, zigzag series, refers to scales on the narrowest region of the caudal peduncle counted from the dorsalmost scale to the ventralmost scale in a zigzag (alternating) manner. Finally, the cephalic neuromast distribution patterns were examined and illustrated with the aid of a dissecting microscope and camera lucida.

Cephalic neuromast patterns

Eleotris species are mainly distinguished by the superficial neuromast patterns of the head (Akihito, 1967). Cephalic neuromast patterns are described using terminology developed by Sanzo (1911) with modifications employed by Miller and Wongrat (1991) and Pezold and Cage (2002). Transverse opercular rows are labelled *ot*. Upper and lower longitudinal rows on the operculum are labelled *os* and *oi*, respectively. Transverse suborbital rows are designated with Arabic numbers and major horizontal rows on the cheek are indicated with the letters *b* and *d*. To simplify references to the particular transverse suborbital rows crossing row *d*, a formula of row numbers separated by periods is used (Mennesson *et al.*, 2019). For example, if rows 2, 4 and 6 cross row *d*, this condition is represented by the formula '2.4.6' (see Fig. 1). Five different patterns have been noted by Mennesson (2016) and Mennesson *et al.* (2019): '2' for the '*Eleotris oxycephala* group' (Fig. 1A); '2.4' for the '*Eleotris acanthopoma* group' (Fig. 1B), '2.3.4' for the '*Eleotris melanoxoma* group' (Fig. 1C), '2.4.6' for the '*Eleotris fusca* group' (Fig. 1D) and '2.4.5.6' for *E. eigenmanni* (Fig. 1E).

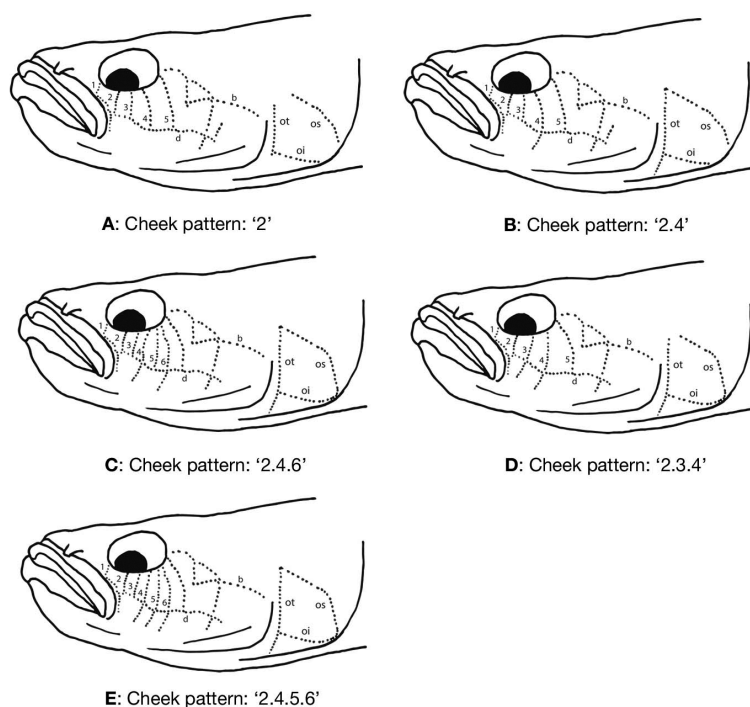


Figure 1. – The five different cephalic neuromast patterns in *Eleotris*.

Genetics

DNA extraction and amplification of partial cytochrome oxidase I gene (*COI*)

Total DNA was extracted using Macherey & Nagel NucleoSpin® Tissue kits following the manufacturer's instructions on an Eppendorf EpMotion 5075.

The DNA of a selection of 32 specimens out of the 62 specimens collected in the Indian Ocean island rivers (Tab. I), the three specimens of *E. melanosoma* collected in Pacific Ocean and from one specimen used as outgroup (*Bunaka gyrinoides*), was amplified for the barcoding fragment of the *COI* gene (584 bp). Five Malagasy specimens were not well preserved and the DNA was too damaged to enable the amplification of the *COI* barcoding fragment. Consequently, for these specimens, primers to amplify a short *COI* fragment (79 bp) were specifically designed in the present study. The 584 bp long *COI* fragment was amplified with the specific fish primers TelF1 and TelR1 (Dettaï *et al.*, 2011) while the 79 pb long *COI* fragment was amplified with primers COI_1F and COI_130R (Tab. IIA). 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 pM; 1.2 µL of DNA extract was added. After denaturation for 2 min at 94°C, the PCR was run for 55 cycles of (25s, 94°C; 25s, 52°C; 55s, 72°C) on a Bio-Rad C1000 Touch Thermal Cycler. Successful PCRs were select-

ed 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.

COI gene analysis

Data processing and sequence assembly were done in Geneious 11.1.2 (<http://www.geneious.com>, Kearse *et al.*, 2012). *COI* sequences were aligned with Muscle Alignment. A phylogenetic tree was performed on the 584 bp alignment using Bayesian inference (MrBayes v.3.2; Ronquist *et al.*, 2012). Three models, corresponding to the three-codon positions, computed in Partition-Finder (Lanfear *et al.*, 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 and 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 sequence of another genera

of Eleotridae, *Bunaka gyrinoides* was included as outgroup. A maximum likelihood tree on the 79 bp alignment was also constructed using MEGA-X (Kumar *et al.*, 2018; Stecher *et al.*, 2020). The model GTR+I+G was run for 1000 bootstrap replications.

For each analysis, the percentage of divergence between sequences was calculated with the Geneious 11.1.2 software.

RESULTS

COI gene

A total of 584 bp of the *COI* gene from 26 *Eleotris* individuals was obtained (Tab. I).

The phylogeny presented two branches separated by 13% of divergence (d). The first one is composed of two species, *E. klunzingerii* (1) and *E. fusca* (2) (d = 5.4%) (Fig. 2A). The second branch presented 3 clades. The first one is composed of one new species *E. diamsoi* (see description in the present work) (3), which has 14% of divergence with the other species of the branch. The two other clades are separated by 13.9% of divergence; one clade is composed of *E. valadei*, a new species (see description in the present work) (4) and *E. melanosoma* (5) (d = 6.9%) while the other clade includes *E. acanthopoma* (6) and *E. pellegrini* (7) (d = 9.9%). Seven species were molecularly distinguished in this phylogeny.

A total of 79 bp of the *COI* gene from 32 individuals were

Table II. – Continued.

C

Nucleotide position	2	6	9	12	15	18	21	27	30	36	39	45	57	61	63	69	78
<i>E. klunzingerii</i>	C	G	A	C	T	T	G	A	C	C	T	A	T	C	A	A	A
<i>E. fusca</i>	T	A	G	C	T	T	A	A	C	C	T	G	T	C	A	A	A
<i>E. melanosoma</i>	C	G	A	C	C	T	A	A	A	C	C	A	T	T	A	A	A
<i>E. valadei</i> n. sp.	C	G	A	C	C	T	A	A	A	C	C	A	T	T	A	G	A
<i>E. diamsoi</i> n. sp.	C	A	A	C	C	C	A	G	C	C	T	A	T	C	A	A	A
<i>E. sahanaensis</i> n. sp.	C	A	A	C	A	C	A	A	G	A	T	A	T	C	A	A	A
<i>E. pellegrini</i>	C	A	A	C	A	C	A	A	G	A	T	A	C	C	G	A	G
<i>E. acanthopoma</i>	C	A	G	T	A	C	A	A	A	T	T	A	C	T	G	A	G

obtained; the 79 bp alignment includes the 26 specimens analysed in the 584 pb alignment plus 5 Malagasy specimens, which were not well preserved. The maximum likelihood tree allowed the validation of an eighth, and new species (Fig. 2b), *E. sahanaensis* (see description in the present work) (8), which has 6.5% of divergence with *E. pellegrini* (7) and *E. acanthopoma* (6) and 9.7% of divergence with *E. diamsoi* (3). The Pairwise distance matrix is presented in Table IIB and the diagnostic nucleotide substitutions for the 79 bp alignment are presented in table IIC.

Morphomeristics

After examination and measurement of 45 type specimens, the morphological and meristic identification of the 65 recent specimens showed that 10 species were present in our samples: four with the pattern ‘2.4’, *E. acanthopoma* Bleeker, 1853 widespread in Indo-Pacific, *E. vomerodentata* Maugé, 1984, from Madagascar, *E. pellegrini* Maugé, 1984 from Madagascar and Seychelles, and a new species *E. sahanaensis* (*E. sp2b*) (see description in the present work) from Madagascar (Tabs III-V); four with the pattern ‘2.3.4’, *E. soaresi* Playfair, 1867, from Mozambique [in the light of this new study, *E. soaresi* is not a synonym of *E. melanosoma* but a valid species], *E. melanosoma* (Bleeker, 1853) [as stated by Mennesson *et al.* (2019), *E. melanosoma* is not present in West Indian Ocean but restricted to Pacific Ocean] and two new species *E. valadei* (*E. sp2*) (see description in the present work) from Madagascar, Mayotte (Comoros), Reunion Island and Seychelles, and *E. diamsoi* (*E. sp5*) (see description in the present work) from Madagascar (Tabs VI-VIII); two with the pattern ‘2.4.6’, *E. fusca* (Bloch & Schneider, 1801), widespread in the Pacific and rare in Indian Ocean and *E. klunzingerii* Pfeffer, 1893 from Madagascar, Mayotte (Comoros), Reunion Island and Seychelles.

Eleotris pellegrini, *E. vomerodentata* and *E. soaresi* are redescribed in this paper.

***Pattern ‘2.4’**

Redescription of *Eleotris pellegrini* Maugé, 1984

***Eleotris pellegrini* Maugé, 1984**

(Figs 1B, 2, 3; Tabs III-V)

Material examined

Syntypes. – MNHN-IC-1932-0108 from Madagascar (1 male and 2 females).

Others. – Fifteen males and five females collected from Seychelles and Madagascar with a size range of 29.3-64 mm SL. MNHN-IC-2007-0204, 2 specimens, Grande Anse, Mahé, Seychelles Islands, 20 Nov. 2004, Accouche *et al.* coll.; tags M-0204A & M-0204B. MNHN-IC-2020-0043, Silhouette, Anse Mondon, Seychelles Islands, 20 Nov. 2004, Accouche *et al.* coll.; tag 13970. MNHN-IC-2007-0200, 2 specimens (tags A, B) of 3, Mahé, Seychelles Islands, 22 Nov. 2004, Accouche *et al.* coll. MNHN-IC-2020-0049, Andrepona, Madagascar, 04 Jul. 08, Diamsoi coll.; tag 7546. MNHN-IC-2020-0050, same data as 2020-0049, tag 7547. MNHN-IC-2020-0051, same data as 2020-0049, tag 7548. MNHN-IC-2020-0052, Ambanizana, Madagascar, May 2010, Diamsoi coll.; tag 13015. MNHN-IC-2020-0053, Farambana, Madagascar, July 2008, Diamsoi coll.; tag 13007. MNHN-IC-2020-0054, Sahana, Madagascar, 07 Jul. 2008; Diamsoi coll.; tag 12947. MNHN-IC-2020-0055, same data as 2020-0053; tag 13001. MNHN-IC-1962-0172, 3 specimens, Madagascar, Lampahana, Kiener coll. MNHN-IC-2020-0056, Fond B’Offay, Praslin, Seychelles Islands, 22 Feb. 2020, Keith, Mennesson, Henriette *et al.*, coll.; tag 12728. MNHN-IC-2020-0057, same data as 2020-0056, tag 12730. MNHN-IC-2020-0058, Grand St Louis River, Mahé, Seychelles Islands, 15 Feb. 2020, Keith, Mennesson, Henriette *et al.*, coll.; tag 12593.

Diagnosis

The species is distinguished by: second and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (‘2.4’ pattern), row *os* not connected with

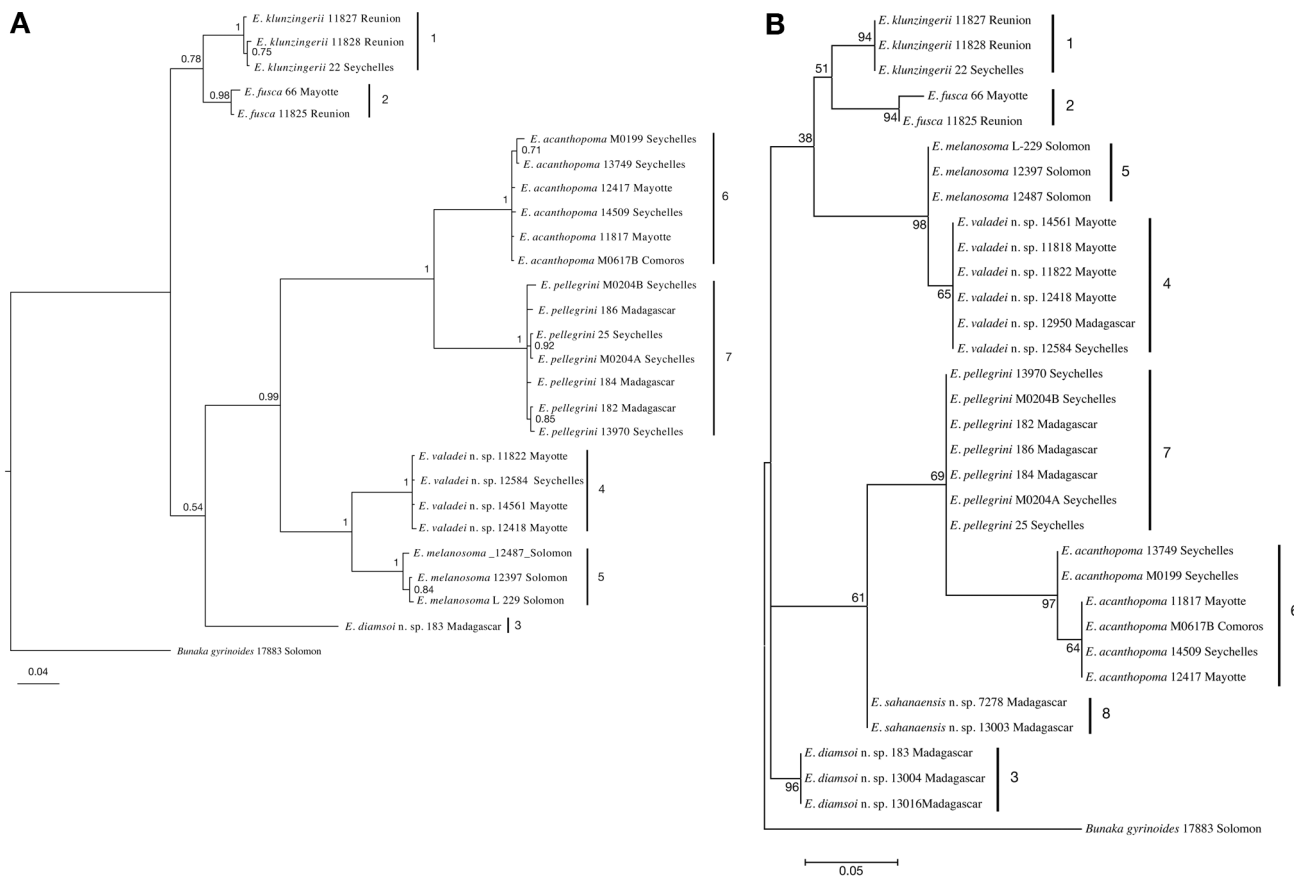


Figure 2. – **A**: Bayesian tree of the *cytochrome c oxidase subunit* (*COI* – 584 bp) for sequenced specimens of *Eleotris*. Numbers at each node represent posterior probabilities. **B**: Maximum Likelihood tree of the *cytochrome c oxidase subunit* (*COI* – 79 bp) for sequenced specimens of *Eleotris*. Numbers at each node represent bootstraps.

row *oi* at ventro-posterior margin of operculum (‘open’ pattern); 15 pectoral fin rays; no teeth on vomer; scales in zigzag series 10-12, and 18-24 in transverse forward series.

Description

Scale and ray counts in *Eleotris pellegrini* and related species are given in tables III-IV, morphometrics in table V.

The body is elongated but stocky. The body depth at anus is 17-24 (% SL) and the caudal peduncle depth is 10-17 (% SL). Predorsal length 42-49 (% SL) and preanal length 62-70 (% SL). Size: up to 64 mm SL.

Head (32-37% SL) slightly depressed, the snout is pointed. Eyes high on head. The mouth is large, as jaw length is 9-14% SL, and oblique, the posterior margin of upper jaw reaches the vertical through the half of the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth, larger on outer row; a few caniniform teeth in posterior position.

Dorsal fins mostly VI-I,8-9; D1 separate from and same height as D2; spines not elongated. Anal fin I,8-9 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 15. Caudal fin rounded with 15 branched rays.



Figure 3. – *Eleotris pellegrini*, Grand St Louis River, Mahe, Seychelles Islands (tag 12592) (© M.I. Mennesson, P. Keith).

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, prepelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. 48-56 scales in lateral series, 28-37 in predorsal series, 14-16 in transverse back series, 18-24 in transverse forward series and 10-12 in zigzag series.

A downward pointing spine at the posterior margin of the

Table III. – Scale counts in *Eleotris* with a ‘2.4’ pattern in the Indian Ocean.

		Lateral series														
		48	49	50	51	52	53	54	55	56	57	58	59	60		
<i>E. acanthopoma</i>	Males						3	1	4	3	1	2	2			
	Females				1	–	2	2	–	–	–	–	–	1		
<i>E. vomerodentata</i>	Males				1											
<i>E. pellegrini</i>	Males		2	–	3	5	1	2	2	1						
	Females	1	1	–	–	1	–	–	–	1						
<i>E. sahanaensis</i>	Male								1							
	Juv-Female							1								
		Predorsal midline series														
		28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>E. acanthopoma</i>	Males			3	1	1	1	–	–	1	3	–	–	1	–	1
	Females				2	1										
<i>E. vomerodentata</i>	Males													1		
<i>E. pellegrini</i>	Males	1	3	4	4	–	1	1								
	Females		1	–	–	1										
<i>E. sahanaensis</i>	Male		1													
	Juv-Female			1												
		Transverse backward series					Zigzag series									
		14	15	16	17	18	10	11	12	13	14					
<i>E. acanthopoma</i>	Males	1	1	8	5	2		5	4	7	1					
	Females		2	3	1			2	1	3						
<i>E. vomerodentata</i>	Males			1				1								
<i>E. pellegrini</i>	Males	6	5	5			3	6	7							
	Females	3	2				4	–	1							
<i>E. sahanaensis</i>	Male		1				1									
	Juv-Female	1					1									
		Transverse forward series														
		18	19	20	21	22	23	24	25	26	27	28	29	30		
<i>E. acanthopoma</i>	Males					3	3	2	2	–	–	–	1	1		
	Females				1	1	–	2								
<i>E. vomerodentata</i>	Males		1													
<i>E. pellegrini</i>	Males		1	7	3	1	1	1								
	Females	1	1	1	–	2										
<i>E. sahanaensis</i>	Male		1													
	Juv-Female			1												

preoperculum is covered with skin. Gill opening is moderately broad, extending to below the preoperculum. Tubular anterior nares overhanging half upper lip, posterior nares open pits.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* (‘2.4’ pattern); row *os* not connected with row *oi* at ventro-posterior margin of operculum (‘open pattern’) (Fig. 1B).

Urogenital papilla in females rounded, elongated and tapered in males.

Colour in life (Fig. 3)

Male and female similar. Body marbled from light to dark brown, more beige on the back and striped and spotty on the flanks, alternating dark brown and beige. Three horizontal dark brown to reddish stripes between eyes and preoperculum and three vertical white ones below the eye. First dorsal fin translucent with two large horizontal dark spotted

Table IV. – Ray counts in *Eleotris* with a ‘2.4’ pattern in the Indian Ocean.

		Pectoral fin rays			
		15	16	17	18
<i>E. acanthopoma</i>	Males		7	10	
	Females		3	3	
<i>E. vomerodontata</i>	Males	1			
<i>E. pellegrini</i>	Males	15	1		
	Females	5			
<i>E. sahanaensis</i>	Male	1			
	Juv-Female	1			
		Second dorsal fin rays			
		1,8	1,9		
<i>E. acanthopoma</i>	Males	5	11		
	Females		6		
<i>E. vomerodontata</i>	Males		1		
<i>E. pellegrini</i>	Males	2	14		
	Females		5		
<i>E. sahanaensis</i>	Male		1		
	Juv-Female	1			
		Anal fin rays			
		1,7	1,8	1,9	
<i>E. acanthopoma</i>	Males		7	9	
	Females			6	
<i>E. vomerodontata</i>	Males		1		
<i>E. pellegrini</i>	Males		8	8	
	Females		2	3	
<i>E. sahanaensis</i>	Male		1		
	Juv-Female			1	

stripes, one at fin base, one in the middle of the fin. Second dorsal and anal fins with 5-6 brownish wavy spotted horizontal stripes. Pelvic fins base yellowish. Caudal fin brown, with two brown spots anteriorly, several brownish vertical spotted wavy rows. Pectoral fins translucent.

Colour in preservation

Male and female similar. Body marbled brown, lighter on the back and striped on the flanks. Three horizontal dark brown stripes between eyes and preoperculum. First dorsal fin with two large horizontal dark stripes, one at fin base, one in the middle of the fin. Second dorsal and anal fins with 5-6 brownish wavy spotted horizontal stripes. Caudal fin brown, with two brown spots anteriorly, several brownish vertical wavy spotted stripes. Pectoral fins greyish.

Comparison

Eleotris pellegrini differs from the other species sequenced that occur in the area studied by having a high % of divergence in *COI* gene (9.4-15.2%).

Within the pattern ‘2.4’ group, *E. pellegrini* differs from

E. acanthopoma in having 15 pectoral fin rays *versus* 16-17 and 28-34 scales in predorsal series *versus* 30-42. It differs from *E. vomerodontata* by the absence of teeth in the vomer *versus* presence. It differs from *E. sahanaensis* by a greater head length (31-37 *versus* 30-32% SL) and more scales in zigzag series (10-12 *versus* 10).

Distribution

Currently known only from Madagascar and the Seychelles Islands. It was found in Seychelles in sympatry with *E. acanthopoma* and in Madagascar with *E. sahanaensis* (this paper).

Ecology

The species is supposed to be mainly amphidromous (Mennesson and Keith, 2017). It lives in the lower part of the river. It lives in muddy to clear rivers with sandy to gravel bottom between 5 to 10 m in altitude. It is carnivorous.

Redescription of *Eleotris vomerodontata* Maugé, 1984

Eleotris vomerodontata Maugé, 1984

(Figs 1B, 2, 4; Tabs III-V)

Material examined

Holotype. – MNHN-IC-1984-0803 from Madagascar (male).

Diagnosis

The species is distinguished by: second and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (‘2.4’ pattern), row *os* not connected with row *oi* at ventro-posterior margin of operculum (‘open’ pattern); 15 pectoral fin rays and the presence of teeth in the vomer.

Description

Scale and ray counts in *Eleotris vomerodontata* and related species are given in tables III-IV, morphometrics in table V.

The body is elongated. The body depth at anus is 21 (% SL) and the caudal peduncle depth is 13 (% SL). Predor-



Figure 4. – *Eleotris vomerodontata*, holotype MNHN-IC-1984-0803 (© M.I. Mennesson).

Table V. – Main morphometrics in *Eleotris* with a ‘2.4’ pattern in the Indian Ocean.

		Jaw length						Caudal peduncle depth							
		9	10	11	12	13	14	10	11	12	13	14	15	16	
<i>E. acanthopoma</i>	Males		2	3	6	5	1			1	1	8	1	6	
	Females			2	3	–	1				2	4			
<i>E. vomerodentata</i>	Males						1				1				
<i>E. pellegrini</i>	Males	3	1	3	2	4	3	1	4	3	1	4	1	1	
	Females		2	1	2					1	3	1			
<i>E. sahanaensis</i>	Male			1						1					
	Juv-Female	1							1						
		Body depth at anus origin													
		14	15	16	17	18	19	20	21	22	23	24	25		
<i>E. acanthopoma</i>	Males					1	2	2	2	1	2	2	1		
	Females						2	2	1	–	–	1			
<i>E. vomerodentata</i>	Males								1						
<i>E. pellegrini</i>	Males				1	2	1	1	2	4	–	3			
	Females							1	–	–	–	1			
<i>E. sahanaensis</i>	Male									1					
	Juv-Female			1											
		Head length													
		26	27	28	29	30	31	32	33	34	35	36	37		
<i>E. acanthopoma</i>	Males						3	4	1	2	4	2			
	Females						1	2	1	1	1				
<i>E. vomerodentata</i>	Males										1				
<i>E. pellegrini</i>	Males							4	4	2	2	2	1		
	Females						1	2	2						
<i>E. sahanaensis</i>	Male							1							
	Juv-Female				1										
		Predorsal length													
		41	42	43	44	45	46	47	48	49	50				
<i>E. acanthopoma</i>	Males	1	3	4	1	2	2	–	1	–	1				
	Females				3	3									
<i>E. vomerodentata</i>	Males							1							
<i>E. pellegrini</i>	Males		1	2	2	4	3	3	2						
	Females				1	1	1	1	–	1					
<i>E. sahanaensis</i>	Male							1							
	Juv-Female						1								
		Prenatal length													
		60	61	62	63	64	65	66	67	68	69	70			
<i>E. acanthopoma</i>	Males	1	–	3	3	3	1	2	1	1	–	1			
	Females			1	2	2	–	–	1						
<i>E. vomerodentata</i>	Males						1								
<i>E. pellegrini</i>	Males			1	5	1	1	1	1	2	1	1			
	Females			2	1	1	–	1							
<i>E. sahanaensis</i>	Male				1										
	Juv-Female		1												

sal length 47 (% SL) and preanal length 65 (% SL).

The head (35 % SL) is depressed, the snout is pointed. Eyes high on head. The mouth is large, as jaw length is 14% SL, and oblique, the posterior margin of upper jaw reaches the vertical through the two third of the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth, larger on outer row in upper jaw, on inner row in lower jaw; a few caniniform teeth in posterior position. Presence of numerous well-marked teeth in half circle on the vomer, larger in the front part.

Dorsal fins VI-I,9; D1 separate from and same height as D2; spines not elongated. Anal fin I,8 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 15. Caudal fin slightly rounded with 15 branched rays.

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, pre-pelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. 51 scales in lateral series, 40 in predorsal series, 16 in transverse back series, 19 in transverse forward series and 11 in zigzag series.

A downward pointing spine at the posterior margin of the preoperculum is covered with skin. Gill opening moderately broad, extending to below the preoperculum. Tubular anterior nares overhanging half upper lip, posterior nares open pits.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* (‘2.4’ pattern); row *os* not connected with row *oi* at ventro-posterior margin of operculum (‘open pattern’) (Fig. 1B).

Urogenital papilla tapered in male.

Colour in life

Unknown.

Colour in preservation (Fig. 4)

Head, preoperculum, body and abdomen beige to light brown. Gular and isthmus clearer, rose to slightly whitish. Fins whitish beige.

Comparison

Within the pattern '2.4' *Eleotris vomerodentata* differs from all other species by the presence of teeth in the vomer *versus* absence.

Distribution

Currently known only from Madagascar.

Ecology

Unknown.

Description of the new species**Comparative material**

Adults with five transverse suborbital free neuromast rows of which second and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* ('2.4' pattern); row *os* not connected with row *oi* at ventro-posterior margin of operculum ('open pattern').

Eleotris acanthopoma: MNHN-IC-2006-0617, 3 specimens, Mohéli, Mdjawaché, Comoros Islands, 31 Oct. 2005, Keith *et al.* coll. MNHN-IC-2020-0029, Mayotte, Kwale, Comoros Islands, 22 Apr. 2009, Feutry coll.; tag 12426. MNHN-IC-2020-0030, Comoros Islands, Mayotte, Apr. 2009, Feutry coll.; tag 12417. MNHN-IC-2020-0031, Mayotte, Ouroveni, Comoros Islands, 06 Sep. 2007, Marquet coll.; tag 13951. MNHN-IC-2020-0032, same data as 2020-0031, 06 Sep. 2007, Marquet coll.; tag 13952. MNHN-IC-2020-0033, same data as 2020-0031; tag 13953. MNHN-IC-2020-0034, same data as 2020-0031; tag 13954. MNHN-IC-2020-0041, Mayotte, Ouroveni, Comoros Islands, 06 Sep. 2007, Marquet coll.; tag 11817. MNHN-IC-2020-0035, Mayotte, Coconi, Comoros Islands, 06 Aug. 19, Valade *et al.* coll.; tag 14519. MNHN-IC-2020-0036, same data as 2020-0035, tag 14520. MNHN-IC-2020-0037, same data as 2020-0035, tag 14521. MNHN-IC-2020-0038, Comoros Islands, Mayotte, Ouroveni, 06 Aug. 2019, Valade *et al.* coll.; tag 14562. MNHN-IC-2020-0039, Comoros Islands, Mayotte, Longoni, 07 Aug. 2019, Valade *et al.* coll.; tag 14563. MNHN-IC-2020-0040, same data as 2020-0039, tag 14564. MNHN-IC-2007-0185, 2 specimens, Mahé, Seychelles Islands, 24 Nov. 2004, Accouche *et al.* coll. MNHN-IC-2007-0199, Mahé, Anse aux poules bleues riv., Seychelles Islands, 14 Oct. 2003, Keith *et al.* coll. MNHN-IC-2007-0205, Praslin, Fond B'Offay riv., Seychelles Islands, 10 Oct. 2003, Keith *et al.* coll.; tag 14509. MNHN-IC-2020-0042, Praslin, Nouvelle découverte, Seychelles Islands, 09 Oct. 2003, Keith *et al.* coll.; tag 13749. MNHN-IC-2007-0200, 1 (tag C) of 3, Mahé, Seychelles Islands, 22 Nov. 2004, Accouche *et al.* coll.

Eleotris vomerodentata Maugé, 1984: holotype from Madagascar (MNHN-IC-1984-0803).

Eleotris pellegrini Maugé, 1984: syntypes from Madagascar (MNHN-IC-1932-0108) and others (see above, *E. pellegrini* redescription).

***Eleotris sahanaensis* sp. nov. Mennesson, Keith & Feunteun**

(Figs 1B, 2, 5; Tabs III-V)

Material examined

One male and one juvenile collected from Madagascar with a size range of 26-44 mm SL.

Holotype. – MNHN-IC-2020-0078, male (44 mm SL), Sahana River, Madagascar; July 2008; Diamsoi coll.; tag 13003.

Paratype. – MNHN-IC-2020-0077, juv. (26 mm SL), Andrepona River, Madagascar; 4 Jul. 2008; Diamsoi coll.; tag 7278.

Diagnosis

The species is distinguished by: second and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* ('2.4' pattern), row *os* not connected with row *oi* at ventro-posterior margin of operculum ('open' pattern); 15 pectoral fin rays; no teeth on vomer; 54-55 scales in lateral series and 29-30 scales in predorsal series.

Description

Scale counts in *Eleotris sahanaensis* sp. nov. and related species are given in table III, ray counts in table IV and morphometrics in table V. Below, the holotype counts are given first followed in brackets, if different, by the paratype counts.

The body is elongated. The body depth at anus is 22 (16% SL) and the caudal peduncle depth is 12 (11% SL). Predorsal length 47 (46% SL) and preanal length 63 (61% SL).

The head 32 (30% SL) is broad and depressed, the snout is pointed. Eyes high on head. The mouth is quite large, as jaw length 11 (9% SL), and oblique, the posterior margin of upper jaw reaches the vertical through the two thirds of the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth.

Dorsal fins VI-I,8-9; D1 separate from and smaller than D2; spines not elongated. Anal fin I,8-9 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 15. Caudal fin pointed with 15 branched rays.

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, prepelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. 55 (54) scales in lateral series, 29 (30) in predorsal series, 15 (14) in transverse back series, 19 (20) in transverse forward series and 10 in zigzag series.

A downward pointing spine at the posterior margin of the preoperculum is covered with skin. Gill opening is moder-

ately broad, extending to below the preoperculum. Tubular anterior nares overhanging half upper lip, posterior nares open pits.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* ('2.4' pattern); row *os* not connected with row *oi* at ventro-posterior margin of operculum ('open pattern') (Fig. 1B).

Urogenital papilla elongated and tapered in male.

Colour in life

Unknown.

Colour in preservation (Fig. 5)

Head and preoperculum greyish, finely spotted and with 3-4 oblique brown lines from the eye to the edge of operculum. Back brown, flanks light brown with numerous dots more or less aligned from the operculum to the hypural. A big blackish area at the anterior part of the flanks, below the medial part. Abdomen and gular region whitish to yellowish and finely spotted. A black dot at the base of the pectoral fins. Anal and second dorsal fins with 3-4 dark horizontal bands alternating with 3 small white ones. Caudal fin greyish, with 2-3 small spots anteriorly. Pelvic fins whitish.

Comparison

Eleotris sahanaensis differs from the other species sequenced that occur in the area studied by having a high % of divergence in *COI* gene [79 bp alignment] (3.8-10.1%).

Within the pattern '2.4', *E. sahanaensis* differs from *E. acanthopoma* in having 15 pectoral fin rays *versus* 16-17, 10 scales in zigzag series *versus* 11-14, and 29-30 scales in predorsal series *versus* 30-42. It differs from *E. vomerodentata* by the absence of teeth in the vomer *versus* presence. It differs from *E. pellegrini* by a smaller head length (30-32 *versus* 31-37% SL) and fewer scales in zigzag series (10 *versus* 10-12).



Figure 5. – *Eleotris sahanaensis* n. sp., Sahana River, Madagascar (tag 13003) (© M.I. Mennesson).

Distribution

Currently known only from Madagascar. It was found in sympatry with *E. pellegrini* and *E. diamsoi* (this paper).

Ecology

Unknown.

Etymology

The new species is named after the Sahana River, type locality, where many species of *Eleotris* were found.

*Pattern '2.3.4'

Redescription of *Eleotris soaresi* Playfair, 1867

Eleotris soaresi Playfair, 1867

(Figs 1D, 2, 6; Tabs VI-VIII)

Material examined

Syntypes: BMNH 1864.11.15.127 (1), 1865.3.18.26-27 (2), 1867.3.9.521 (1) from Mozambique.

Diagnosis

The species is distinguished by: second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* ('2.3.4' pattern), row *os* connected with row *oi* at ventro-posterior margin of operculum ('closed' pattern); 17-18 pectoral fin rays; 50-56 scales in lateral series, and 12-13 scales in zigzag series.

Description

Scale and ray counts in *Eleotris soaresi* and related species are given in tables VI-VII and morphometrics in table VIII.

The body is elongated. The body depth at anus is 20-21 (% SL) and the caudal peduncle depth is 15 (% SL). Predorsal length 47 (% SL) and preanal length 65-69 (% SL). Size: up to 100 mm SL.

The head (33-37% SL) is broad and depressed, the snout is pointed. Eyes high on head. The mouth is large, as the jaw length is 11-13% SL, and oblique, the posterior margin of upper jaw reaches the vertical through the two thirds of

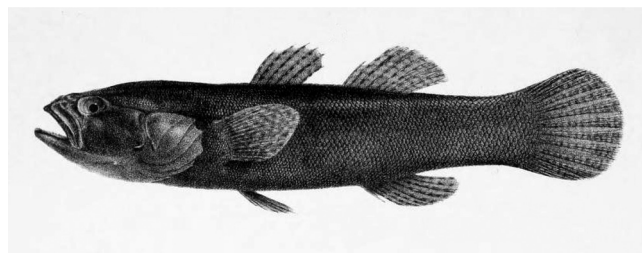


Figure 6. – *Eleotris soaresi*, in Playfair and Günther, 1867.

Table VI. – Scale counts in *Eleotris* with a ‘2.3.4’ pattern in the Indian Ocean.

		Lateral series																			
		50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
<i>E. soaresi</i>	Male	1	–	–	–	1	–	1													
<i>E. valadei</i> n. sp.	Male									1	–	2	–	2							
	Female									1	–	–	–	1							
<i>E. diamsoi</i> n. sp.	Male														1						
	Female														1						
		Predorsal midline series																			
		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>E. soaresi</i>	Male								1	–	–	–	1								
<i>E. valadei</i> n. sp.	Male														1	–	–	1	1	1	
	Female						1														
<i>E. diamsoi</i> n. sp.	Male							1													
	Female								1												
		Transverse backward series										Zigzag series									
		15	16	17	18	19	20	21	22	12	13	14	15								
<i>E. soaresi</i>	Male	1	–	1	1					1	2										
<i>E. valadei</i> n. sp.	Male			1	1	–	2	1			2	2	1								
	Female			1	–	–	1				1	–	1								
<i>E. diamsoi</i> n. sp.	Male				1							1									
	Female				1							1									
		Transverse forward series																			
		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30					
<i>E. soaresi</i>	Male							1	–	1											
<i>E. valadei</i> n. sp.	Male												1	2	1	1					
	Female													1	–	1					
<i>E. diamsoi</i> n. sp.	Male		1																		
	Female								1												

the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth.

Dorsal fins VI-I,8-9; D1 separate from and same height as D2; spines not elongated. Anal fin I,8-9 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 17-18. Caudal fin rounded with 15 branched rays.

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, prepelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. 50-56 scales in lateral series; 39-43 in predorsal series, 15-18 in transverse back series, 22 in transverse forward series and 12-13 in zigzag series.

A downward pointing spine at the posterior margin of the preoperculum is covered with skin. Gill opening is moderately broad, extending to below the preoperculum.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second, third and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* (‘2.3.4’ pattern); row *os* connected with row *oi* at ventro-posterior margin of operculum (‘closed pattern’) (Fig. 1C).

Urogenital papilla elongated and tapered in males.

Table VII. – Ray counts in *Eleotris* with a ‘2.3.4’ pattern in the Indian Ocean.

		Pectoral fin rays				
		15	16	17	18	19
<i>E. soaresi</i>	Male			1	2	
	Female				5	
<i>E. valadei</i> n. sp.	Male				2	
	Female					
<i>E. diamsoi</i> n. sp.	Male		1			
	Female		1			
		Anal fin rays		Sec. dorsal fin rays		
		1,8	1,9	1,8	1,9	
<i>E. soaresi</i>	Male	1	2		3	
<i>E. valadei</i> n. sp.	Male	3	2	2	3	
	Female	2		2		
<i>E. diamsoi</i> n. sp.	Male	1		1		
	Female	1		1		

Table VIII. – Main morphometrics in *Eleotris* with a ‘2.3.4’ pattern in the Indian Ocean.

		Jaw length									
		9	10	11	12	13	14	15			
<i>E. soaresi</i>	Male			1	–	1					
<i>E. valadei</i> n. sp.	Male				2	1	1	1			
	Female			1	1						
<i>E. diamsoi</i> n. sp.	Male	1									
	Female			1							
		Body depth at anal fin origin									
		15	16	17	18	19	20	21	22	23	24
<i>E. soaresi</i>	Male						1	1			
<i>E. valadei</i> n. sp.	Male					1	1	1	–	–	2
	Female							1	1		
<i>E. diamsoi</i> n. sp.	Male	1									
	Female				1						
		Head length									
		31	32	33	34	35	36	37	38	39	40
<i>E. soaresi</i>	Male			1	–	–	–	1			
<i>E. valadei</i> n. sp.	Male			3	–	1	–	–	–	1	
	Female			1	1						
<i>E. diamsoi</i> n. sp.	Male	1									
	Female			1							
		Predorsal length									
		42	43	44	45	46	47	48	49		
<i>E. soaresi</i>	Male						2				
<i>E. valadei</i> n. sp.	Male				2	2	–	–	1		
	Female	1	1								
<i>E. diamsoi</i> n. sp.	Male			1							
	Female						1				
		Preanal length									
		63	64	65	66	67	68	69	70		
<i>E. soaresi</i>	Male			1	–	–	–	1			
<i>E. valadei</i> n. sp.	Male				1	2	1	–	1		
	Female					1	1				
<i>E. diamsoi</i> n. sp.	Male	1									
	Female				1						

Colour in life (Fig. 6)

According to Playfair (*in* Playfair and Günther, 1867) ‘body dark brown, dorsal and anal punctulated with black’.

Colour in preservation

Head, preoperculum, body, abdomen and fins dark brown. Gular and isthmus beige or dark brown depending on the specimen.

Comparison

E. soaresi differs from the other species of Indian Ocean with a ‘2.3.4’ pattern in having fewer scales in lateral series

(50-56 versus 59-64) and in zigzag series (12-13 versus 13-15). Moreover, it differs from *E. valadei* n. sp., this paper, in having fewer scales in transverse forward series (22-24 versus 27-30) and predorsal series (39-43 versus 45-50), and from *E. diamsoi* in having 17-18 pectoral fin rays versus 16.

Distribution

Currently known only from Mozambique.

Ecology

Unknown.

Description of the new species

Comparative material

Adults with five transverse suborbital free neuromast rows of which second, third and fourth suborbital free neuromast rows on cheek extend ventrally past horizontal row *d* (‘2.3.4’ pattern); row *os* connected with row *oi* at ventro-posterior margin of operculum (‘closed pattern’):

Eleotris melanosoma Bleeker, 1853: 2 syntypes from Ceram, Indonesia (*in* RMNH 4815). [synonyms: *Culius insulindicus* Bleeker, 1875: syntypes from Sumatra, Indonesia (RMNH 4804). *Eleotris pseudacanthopomus* Bleeker, 1853: holotype from Western Sumatra, Indonesia (SMNS 10595). *Eleotris melanura* Bleeker, 1849: holotype from southern Java, Indonesia (*in* RMNH 5182)].

Culius macrolepis Bleeker, 1875: syntypes from Ambon, Indonesia (RMNH 4759).

Eleotris soaresi Playfair, 1867: syntypes from Mozambique, Africa (BMNH 1865.3.18.26-27).

***Eleotris diamsoi* sp. nov. Mennesson, Keith & Feunteun**
(Figs 1D, 2, 7; Tabs VI-VIII)

Material examined

One male and one female collected from Madagascar with a size range of 61-64.6 mm SL.

Holotype. – MNHN-IC-2020-0068, male (64.6 mm SL), Sahana River, Madagascar; 7 July 2008; Diamsoi coll.; tag 13004.

Paratype. – MNHN-IC-2020-0067, female (61 mm SL), Ankazofotsy River, Madagascar; May 2010; Diamsoi coll.; tag 13016.

Diagnosis

The species is distinguished by: second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (‘2.3.4’ pattern) (Fig. 1D); row *os* connected with row *oi* at ventro-posterior margin of operculum (‘closed’ pattern); 16 pectoral fin rays; 63 scales in lateral series; a small body depth at anal and second dorsal fins origin (15-18% SL).

Description

Scale counts in *Eleotris diamsoi* sp. nov. and related species are given in table VI, ray counts in table VII and morphometrics in table VIII. Below, the holotype counts are given first followed in brackets, if different, by the paratype counts.

The body is elongated. The body depth at anus is 15 (18% SL) and the caudal peduncle depth is 12 (14% SL). Predorsal length 44 (47% SL) and preanal length 63 (66% SL).

The head 32 (33% SL) is broad and depressed, the snout is pointed. Eyes high on head. The mouth is quite large, as jaw length is 10 (11% SL), and oblique, the posterior margin of upper jaw reaches the vertical through the two thirds of the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth, larger on outer row; a few caniniform teeth in anterior position on lower jaw.

Dorsal fins VI-I,8; D1 separate from and smaller than D2; spines not elongated. Anal fin I,8 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 16. Caudal fin pointed with 15 branched rays.

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, prepelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. 63 scales in lateral series, 36 (38) in predorsal series, 18 in transverse back series, 17 (23) in transverse forward series and 14 in zigzag series.

A downward pointing spine at the posterior margin of the preoperculum is covered with skin. Gill opening is moderately broad, extending to below the preoperculum. Tubular anterior nares overhanging one third of upper lip, posterior nares open pits.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* ('2.3.4' pattern); row *os* connected with row *oi* at ventro-posterior margin of operculum ('closed' pattern) (Fig. 1D).

Urogenital papilla in females rounded, elongated and tapered in males.

Colour in life

Unknown.

Colour in preservation (Fig. 7)

Male and female similar. Head and preoperculum beige. Back and flanks brownish. A big brown dot at the base of the pectoral fins. Abdomen and gular region yellowish. Anal and first and second dorsal fins spotted with spots aligned on rays. Caudal fin brownish, with several yellow spots. Pelvic and pectoral fins whitish.

Comparison

Eleotris diamsoi differs from the other species sequenced that occur in the area studied by having a high % of divergence in *COI* gene (9.9-14.9%).

Eleotris diamsoi n. sp. differs from the other species of the Indian Ocean with a '2.3.4' pattern by several characters. It differs from *E. soaresi* in having 16 pectoral fin rays versus 17-18, more scales in lateral series (63 versus 50-56) and in zigzag series (14 versus 12-13), and a smaller body depth at anal fin origin (15-18 versus 20-21). It differs from *E. valadei*, this paper, in having 16 pectoral fin rays versus 18, fewer scales in predorsal series in males (36-38 versus 45-50), fewer scales in transverse forward series (17-23 versus 27-30) and a smaller body depth at anal fin origin (15-18 versus 19-24).

Distribution

Currently known only from Madagascar. It was found in sympatry with *E. pellegrini* and *E. sahanaensis* (this paper).

Ecology

Unknown.

Etymology

The new species is named after the MNHN 'Diamsoi' program which enabled to collect the specimens in Madagascar.

Eleotris valadei sp. nov. Keith, Mennesson & Henriette (Figs 1D, 2, 8; Tabs VI-VIII)

Material examined

Five males and two females collected from Mayotte, Praslin (Seychelles), Reunion Island and Madagascar, with a size range of 45-99.3 mm SL.

Holotype. – MNHN-IC-2020-0063, male (57 mm SL), Ouroveni River, Mayotte; 06 Aug. 2019; Valade coll.; tag 14561.

Paratypes. – MNHN-IC-2020-0060, male (60.6 mm SL), Ambodiforaha River, Madagascar; Jul. 2008; diamsoi coll.; tag 12950. MNHN-IC-2020-0062, male (45 mm SL), Ourov-



Figure 7. – *Eleotris diamsoi* n. sp., Ankazofotsy, Madagascar (© P. Keith).

eni River, Mayotte; 20 Apr. 2009; Feutry coll.; tag 11822. MNHN-IC-2020-0059, male (46 mm SL), Mtchangachehi, Mayotte; 12 Dec. 2003; tag 12418. MNHN-IC-2020-0061, female (48 mm SL), Ouveveni river, Mayotte; date 06 Aug. 2007; Marquet coll.; tag 11818. MNHN-IC-2020-0064, female (79.3 mm SL), Reunion Island, Dec. 2007, Zimmermann *et al.* coll.; tag 12409. MNHN-IC-2020-0065, male (99.3 mm SL), Nouvelle-Découverte River, Praslin, Seychelles; 21 Feb. 2020; Keith, Mennesson, Henriette *et al.* coll.; tag 12584.

Non types. – MNHN-IC-1966-0959, two males (105–110 mm), Anjanambo, Tamatave Province, Madagascar, Dec. 1962, Kiener & Therezien coll.

Diagnosis

The species is distinguished by: second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* ('2.3.4' pattern), row *os* connected with row *oi* at ventro-posterior margin of operculum ('closed' pattern); 18 pectoral fin rays; 59–64 scales in lateral series and 27–30 scales in transverse forward series.

Description

Scale counts in *Eleotris valadei* sp. nov. and related species are given in table VI, ray counts in table VII and morphometrics in table VIII. Below, the holotype counts are given first followed in brackets, if different, by the paratype counts.

The body is elongated. The body depth at anus is 21 (19–24% SL) and the caudal peduncle depth is 14 (13–17% SL). Predorsal length 45 (42–49% SL) and preanal length 66 (67–70% SL).

The head 33 (33–39 % SL) is broad and depressed, the snout is pointed. Eyes high on head. The mouth is large, as the jaw length is 12 (11–15% SL), and oblique, the posterior margin of upper jaw reaches the vertical through the two thirds of the eye. Upper and lower jaws with multiple rows of small inwardly curved teeth; larger on outer row on upper jaw and larger on inner jaw on lower jaw; a few small caniniform teeth in posterior position.

Dorsal fins VI-I,8-9; D1 separate from and slightly higher than D2; spines not elongated. Anal fin I,8-9 and directly opposite to second dorsal fin. Pelvic fins separate, I,5. Pectoral fins 18. Caudal fin pointed with 15 branched rays.

Cycloid scales on top of head, nape, cheek, operculum, pectoral fin base, prepelvic region, and abdomen. Ctenoid scales covering flanks. No lateral line canals. Scales in lateral series 63 (59–64), in predorsal series 50 (45–49). Scales in transverse back series 21 (17–20), in transverse forward series 30 (27–30) and 13 (14–15) in zigzag series.

A downward pointing spine at the posterior margin of the preoperculum is covered with skin. Gill opening is moderately broad, extending to below the preoperculum. Tubular

anterior nares overhanging upper lip, posterior nares open pits.

Cephalic lateralis: Adults with five transverse suborbital free neuromast rows of which second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* ('2.3.4' pattern); row *os* connected with row *oi* at ventro-posterior margin of operculum ('closed' pattern) (Fig. 1D).

Urogenital papilla in females rounded, elongated and tapered in males.

Colour in life (Fig. 8)

Male and female similar. Top of head, top of the eye and back beige with brown freckles. Lateral part of head and body dark brown. Abdomen and gular region dark brown. Lips with dark brown with evenly spaced yellow spots. First dorsal fin with 2–3 large horizontal dark bands alternating with 2 white bands; rays with yellow to orange spotted wavy rows alternating with black. Second dorsal, anal and pelvic fins with yellow to orange spotted wavy rows alternating with black. Caudal fin dark brown, with in the superior part, at anterior position, a small beige and black striped area. Pectoral fins translucent grey, pectoral base dark brown.

Colour in preservation

Male and female similar. Head and body dark brown. Abdomen and gular region dark brown. First dorsal fin with 2–3 large horizontal dark bands alternating with 2 greyish bands; rays with greyish spots alternating with black wavy spotted rows. Second dorsal, anal and pelvic fins with greyish spots alternating with black wavy spotted rows. Caudal fin dark brown, with in the superior part, at anterior position, a small beige and black striped area. Pectoral fins greyish, pectoral base dark brown.

Comparison

Eleotris valadei differs from the other species sequenced that occur in the area studied by having a high % of divergence in *COI* gene (6.8–14.6%).

Eleotris valadei n. sp. differs from the other species of the Indian Ocean with a '2.3.4' pattern by several characters. It differs from *E. soaresi* in having more scales in lateral series (59–64 *versus* 50–56), more scales in transverse forward series (27–30 *versus* 22–24), in predorsal series (45–50 *versus* 39–43) and in zigzag series (13–15 *versus* 12–13). It differs from *E. diamsoi* n. sp., this paper, in having 18 pectoral fin rays *versus* 16, more scales in transverse forward series (27–30 *versus* 17–23), in predorsal series (45–50 *versus* 36–38), and a higher body depth at dorsal fin origin (19–24 *versus* 15–18).



Figure 8. – *Eleotris valadei* n. sp., MNHN-IC-2020-0065, paratype, Nouvelle-Découverte River, Praslin, Seychelles Islands (tag 12584) (© M.I. Mennesson, P. Keith).



Figure 10. – *Eleotris klunzingerii*, Reunion Island (© E. Vigneux).



Figure 9. – *Eleotris acanthopoma*, Athanas River, Mahe, Seychelles Islands (© P. Keith).



Figure 11. – *Eleotris fusca*, Rarotonga, Cook Islands (© P. Keith).

Distribution

Currently known from Madagascar, Reunion Island, Mayotte and the Seychelles islands. It was found in Seychelles in sympatry with *E. pellegrini* and *E. acanthopoma*.

Ecology

The species is supposed to be amphidromous. It is found in the lower part of the river, near the estuary. It lives in muddy to clear rivers with sandy to gravel bottom between 0 to 5 meters in altitude. It is carnivorous.

Etymology

The name of the species honours Pierre Valade, who collected several specimens of this new species in Reunion Island and Mayotte.

Key of *Eleotris* species from the West Indian Ocean

- 1-a. – Cephalic neuromast pattern ‘closed; ‘2.4.6’ 2
- 1-b. – Cephalic neuromast pattern ‘open; ‘2.4’ 3
- 1-c. – Cephalic neuromast pattern ‘closed; ‘2.3.4’ 6
- 2-a. – Transverse scales in forward series in males 18-30 and females 22-28 *Eleotris klunzingerii* (Fig. 10)
- 2-b. – Transverse scales in forward series in males 13-22 and females 13-25 *Eleotris fusca* (very rare in the West Indian Ocean) (Fig. 11)

- 3-a. – Presence of ‘teeth’ in the vomer *Eleotris vomerodentata* (Fig. 4)
- 3-b. – Absence of ‘teeth’ in the vomer 4
- 4-a. – Pectoral rays 16-17, predorsal scales 30-42 *Eleotris acanthopoma* (Fig. 9)
- 4-b. – Pectoral rays 15, predorsal scales 26-34 5
- 5-a. – Head length 30-32% SL, zigzag scales 10 *Eleotris sahanaensis* n. sp. (Fig. 5)
- 5-b. – Head length 31-37% SL, zigzag scales 10-12 *Eleotris pellegrini* (Fig. 3)
- 6-a. – Lateral scales 50-56, zigzag scales 12-13 *Eleotris soaresi* (Fig. 6)
- 6-b. – Lateral scales 59-69, zigzag scales 13-15 7
- 7-a. – Pectoral rays 16, predorsal scales 36-38 *Eleotris diamsoi* n. sp. (Fig. 7)
- 7-b. – Pectoral rays 18, predorsal scales 45-50 *Eleotris valadei* n. sp. (Fig. 8)

Acknowledgments. – This study was supported by the team BOREA, the French Ichthyological Society (SFI), the MNHN and the Office Français de la Biodiversité. For Seychelles Islands, we would like to particularly thank our friend E. Henriette from Gaea who very efficiently organized the 2020 trip, the PS Alain Decomard, Department of Environment, Mrs Marie-May Muzunguile and Ashley Dias, Biodiversity Conservation and Management Division, Elvis Nicette, Seychelles Bureau of Standards, Mr Dan-

iel Etongo and Nuette Gordon, University of Seychelles; we would also like to thank, for their help on the field, P. Atienza Gonzalez (Gaea), S. Morgan, F. Lesperance, D. Dina, A. Lucas, L. Hoareau (CAMS), V. Banane, E. Lafortune, N. Khan, A. Hector, T. Payet, M. Griffith, K. Collins, I. Dubois, E. Morel, C. Tragett, J. Moumou (SIF), R. Phillipin (MCSS) and Wilna Accouche (Gaea). Thanks to the Environment, Energy & Climate Change (MEECC), for agreeing to the transfer of material. For the Comoros, we would particularly like to thank Yahaya Ibrahim (CNDRS). For Madagascar, we are grateful to J. Aride from Madagascar National Parks (MNP-ANGAP), to the Manager of Masoala National Parc at Maroantsetra, and to the DIAMSOI team (research financed by the Institut Français de la Biodiversité (IFB)), and particularly to his coordinator E. Feunteun (MNH). For Reunion Island and Mayotte, we thank the Environment Offices, Ocea Consult (P. Valade), Arda and the Agriculture Offices. For the loan of specimens we thank: D. Catania (CAS), R. de Ruiter & E. Dondorp (RMNH), S. Dorow, H. Zetzsche, T.J. Alpermann and F. Krupp (SMF), S. Morrison and G.R. Allen (WAM), S. Merker (SMNS), I. Eidus (ZMH), T. Heath and J. Maclaine (BMNH), L. Parenti, J. Williams, L. Palmer and S. Raredon (USNM), M. Hammer and G. Dally (NTM), Z. Gabsi, J. Pfliger, R. Causse, P. Pruvost, (MNH). The authors thank two anonymous reviewers for their useful comments.

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