New record of Ectreposebastes niger (Fourmanoir, 1971) (Setarchidae, Scorpaeniformes): a rare bathypelagic fish from La Perouse Seamount, Western Indian Ocean, and distribution of Ectreposebastes Garman, 1899 in the Indian Ocean

Evgeny Romanov, Yves Cherel, Francis Marsac

New record of Ectreposebastes niger (Fourmanoir, 1971) (Setarchidae, Scorpaeniformes): a rare bathypelagic fish from La Pérouse Seamount, Western Indian Ocean, and distribution of Ectreposebastes Garman, 1899 in the Indian Ocean

Authors: Romanov, Evgeny V., Cherel, Yves, and Marsac, Francis

Source: Zoosystema, 43(15) : 283-296

Published By: Muséum national d'Histoire naturelle, Paris

URL: https://doi.org/10.5252/zoosystema2021v43a15

New record of *Ectreposebastes niger* (Fourmanoir, 1971) (Setarchidae, Scorpaeniformes): a rare bathypelagic fish from La Pérouse Seamount, Western Indian Ocean, and distribution of *Ectreposebastes* Garman, 1899 in the Indian Ocean

Evgeny V. ROMANOV
CAP RUN – CITEB (Centre technique de recherche et de valorisation des milieux aquatiques),
Magasin n°10 – Port Ouest, F-97420 Le Port, Île de la Réunion (France)
evgeny.romanov@citeb.re (corresponding author)

Yves CHEREL
Centre d'Études biologiques de Chizé, UMR 7372 du CNRS-La Rochelle Université,
F-79360 Villiers-en-bois (France)
cherel@cebc.cnrs.fr

Francis MARSAC
MARBEC, Université Montpellier, CNRS, Ifremer, IRD,
avenue Jean-Monnet, CS 30171, F-34203 Sète cedex (France)
and IRD, Seychelles Fishing Authority, Fishing Port, P.O Box 449, Victoria, Mahe (Seychelles)
francis.marsac@ird.fr

Submitted on 28 January 2020 | Accepted on 9 September 2020 | Published on 1 June 2021

urn:lsid:zoobank.org:pub:92D06722-9F7C-4D14-922D-29D15F8C4C0E

Romanov E. V., Cherel Y. & Marsac F. 2021. — New record of *Ectreposebastes niger* (Fourmanoir, 1971) (Setarchidae, Scorpaeniformes): a rare bathypelagic fish from La Pérouse Seamount, Western Indian Ocean, and distribution of *Ectreposebastes* Garman, 1899 in the Indian Ocean. *Zoosystema* 43 (15): 283-296. https://doi.org/10.5252/zoosystema2021v43a15. http://zoosystema.com/43/15

ABSTRACT

A new record of a rare deep-water scorpionfish *Ectreposebastes niger* (Fourmanoir, 1971), is described from the south-western Indian Ocean. This is the ninth record in the Indian Ocean and the first documented record of this species in the waters of Reunion Island. It is also the first record of this species in the Indian Ocean since 1982. Its congener, *Ectreposebastes imus* Garman, 1899 is more common: together with non-published records from museums and online databases the number of verified Indian Ocean records exceeds 15 individuals. Both species are pseudo-oceanic, usually associated with continental and peri-insular slopes and seamounts between 200 and 1300 m depth, occupying a wide range of habitats from demersal to pelagic in the meso- and bathypelagic zones.

KEY WORDS
Deepwater habitat,
pseudo-oceanic species,
pelagic occurrence,
fish morphology,
otoliths,
genetic analysis,
new record.

RÉSUMÉ

*Nouvelle signalisation d'*Ectreposebastes niger *(Fourmanoir, 1971) (Setarchidae, Scorpaeniformes) : un rare poisson bathypélagique du mont sous-marin La Pérouse, océan Indien occidental, et répartition d'*Ectreposebastes *Garman, 1899 dans l'océan Indien.*

Le rare poisson pélagique *Ectreposebastes niger* (Fourmanoir, 1971) est nouvellement signalé du sud-ouest de l'océan Indien, près de l'île de la Réunion. Il s'agit de la neuvième signalisation dans l'océan Indien, la première dans les eaux de l'île de la Réunion, et la première dans l'océan Indien depuis 1982. L'espèce congénérique *Ectreposebastes imus* Garman, 1899 est plus commune : 15 individus sont mentionnés dans l'océan Indien après analyse de la littérature scientifique, des collections de musées et/ou des bases de données en ligne. Les deux espèces sont pseudo-océaniques étant normalement associées avec les pentes continentales et péri-insulaires et les monts sous-marins entre 200 et 1300 m de profondeur, où elles occupent une large gamme d'habitats démersaux à semi-pélagiques dans les zones méso- et bathypélagiques.

MOTS CLÉS
Habitat en eau profonde,
espèce pseudo-océanique,
signalisation pélagique,
morphologie des poissons,
otolithes,
analyse génétique,
signalisation nouvelle.

INTRODUCTION

The pelagic scorpionfish *Ectreposebastes niger* (Fourmanoir, 1971) is a rare deep-water species that inhabits meso- and bathypelagic environments in the Pacific and Indian Oceans (Fourmanoir 1971; Paulin 1982; Mandrytsa 1990; Allen *et al.* 2006; Motomura & Struthers 2015). Biology, ecology, habitat and geographic distribution of *E. niger* are still poorly known. This species occasionally occurs in catches of midwater and demersal trawls deployed during commercial and research fishing operations. It was identified and described relatively recently by Fourmanoir (1971) as *Pontinus niger.* Its validity, however, was immediately challenged: Collette & Uyeno (1972) synonymized *P. niger* with *Ectreposebastes imus* Garman, 1899. While doubts on the identity of *E. niger* and *E. imus* were expressed by Eschmeyer & Randall (1975) and by Paulin (1982) (the latter referring to W. N. Eschmeyer pers. comm), the validity of *P. niger* was re-established some 20 years later (Mandrytsa 1990) preserving its place in the genus *Ectreposebastes* Garman, 1899 (WoRMS Editorial Board 2020). Hence, the genus currently includes two closely-related species: *E. imus* Garman, 1899 (midwater scorpionfish) and *E. niger*. Scale size and counts as well as proportions of body depth, caudal peduncle, dorsal and pectoral fins, and preopercular spine size are the few morphological characters that allow these species to be distinguished from each other (Eschmeyer & Randall 1975; Mandrytsa 1990).

Ectreposebastes imus was considered as a single valid species between 1972 and 1990. Therefore, most records of *E. imus* reported during that period may represent either of the two species.

The midwater scorpionfish *E. imus* is relatively common but not abundant: numerous records of a single or few individuals are known throughout the global oceans from temperate and tropical waters (Eschmeyer & Collette 1966; Eschmeyer & Randall 1975; Fourmanoir 1976; Moser *et al.* 1977; Eschmeyer 1986; Mandrytsa 1990; Poss & Eschmeyer 2002; Bianchi *et al.* 2004; Balanov *et al.* 2009; Escánez & Brito 2011; Hashim 2012; Govindam *et al.* 2013; González *et al.* 2014; Froese & Pauly 2019; Eduardo *et al.* 2019). However, because of the similarity between *E. niger* and *E. imus*, their synonymisation in the past, and as the re-establishment of *E. niger* was published in Russian (Mandrytsa 1990), which may have delayed the recognition of *E. niger*'s validity, the distribution and habitat of both species remain obscure at least in the Indo-Pacific.

In the Indian Ocean, both species are known from a few published records. Three individuals of *E. niger* were reported as *Ectreposebastes* sp. from the Mozambique Channel and Saya-de-Malha Bank by Scherbachev *et al.* (1978), and four other individuals from the Saya-de-Malha Bank and the eastern Indian Ocean by Mandrytsa (1990) (Fig. 1).

Similarly, two specimens of *E. imus* were reported from the Saya-de-Malha Bank and the eastern Indian Ocean by Mandrytsa (1990). Two other individuals from the Arabian Sea and the Bay of Bengal were indicated by Hashim (2012) and two individuals from the Andaman Sea were described by Kawai *et al.* (2017). Non-georeferenced sources mentioned the presence of this species off Indonesia (Pauly *et al.* 1996) and along the south-west coast of India (Govindam *et al.* 2013).

Here we describe a new record of *E. niger* from the pelagic zone of the tropical southwestern Indian Ocean. Then, we discuss the regional distribution and habitat of both *E. niger* and *E. imus* based on published data, museum collection inventories accessible from online databases, and other online sources. We also present the first description of otolith shape for *E. niger* and results of genetic sequencing of this species.

MATERIAL AND METHODS

One individual of *Ectreposebastes niger* (183 mm total length (TL); 165 mm standard length (SL) (Fig. 2) was caught on 18 September 2016 in a midwater trawl by the *R/V Antea* during the LA PÉROUSE research cruise (https://doi.org/10.17600/16004500). The authors were onboard during the capture, collecting fishing and environmental data, and preserved the specimen. The capture position lay between 19°45.84'S, 54°05.28'E and 19°41.43'S, 54°03.80'E (respectively start and end positions of trawling). This midwater trawl was operated in the proximity of La Pérouse Seamount, a steep underwater topographic feature of the southwestern Indian Ocean with an average minimum depth of about 60 m, a crescent-like shape and a length of 12 km along its largest extension (Marsac *et al.* 2020). The seamount is situated at 90 nautical miles (nmi) (*c.* 160 km) northwest of the Reunion Island, France (Fig. 1).

The research midwater trawl was an 'International Young Gadoid Pelagic Trawl' (IYGPT) with a horizontal opening of 15.8 m and a vertical opening of 8 m. A cod-end of 5 mm stretched mesh was used. The trawl was towed horizontally at 3 knots (*c.* 1.5 m s^{-1}) with a target fishing depth of 500 m, although the range of fished depths was 485-590 m during the set that captured the specimen. The tow was performed between 17:46 (trawl at fishing depth) and 18:55 (trawl at the surface) local time (GMT+3) with total duration 69 min.

Sea surface temperature (SST) measured during vertical profiling of the water column with CTD probe was 23.6°C, and the temperature at 500 m depth was 10.4°C.

The ocean floor topography (Marsac *et al.* 2020) shows that the trawl haul was performed over the depths 1400-3000 m at a distance of less than 8 nmi (*c.* 15 km) west of La Pérouse seamount.

The fish was photographed on board (Fig. 2) with a Nikon D7100 digital camera, resolution 24 Mpx, and TL and SL were measured. Otoliths were extracted onboard, cleaned and stored dry separately. After measurement, the specimen was stored frozen at –18°C for *c.* 90 days, then was thawed for 12 hours before examination. After measurements, weighing and sampling (muscle samples were taken for DNA analysis) the fish was preserved in 10% neutral buffered formaldehyde for 48 hours, soaked in freshwater for 4 hours and transferred to 70% ethanol. The specimen was deposited in the collection of the Museum national d'Histoire naturelle, Paris (catalogue number MNHN-IC-2019-0078).

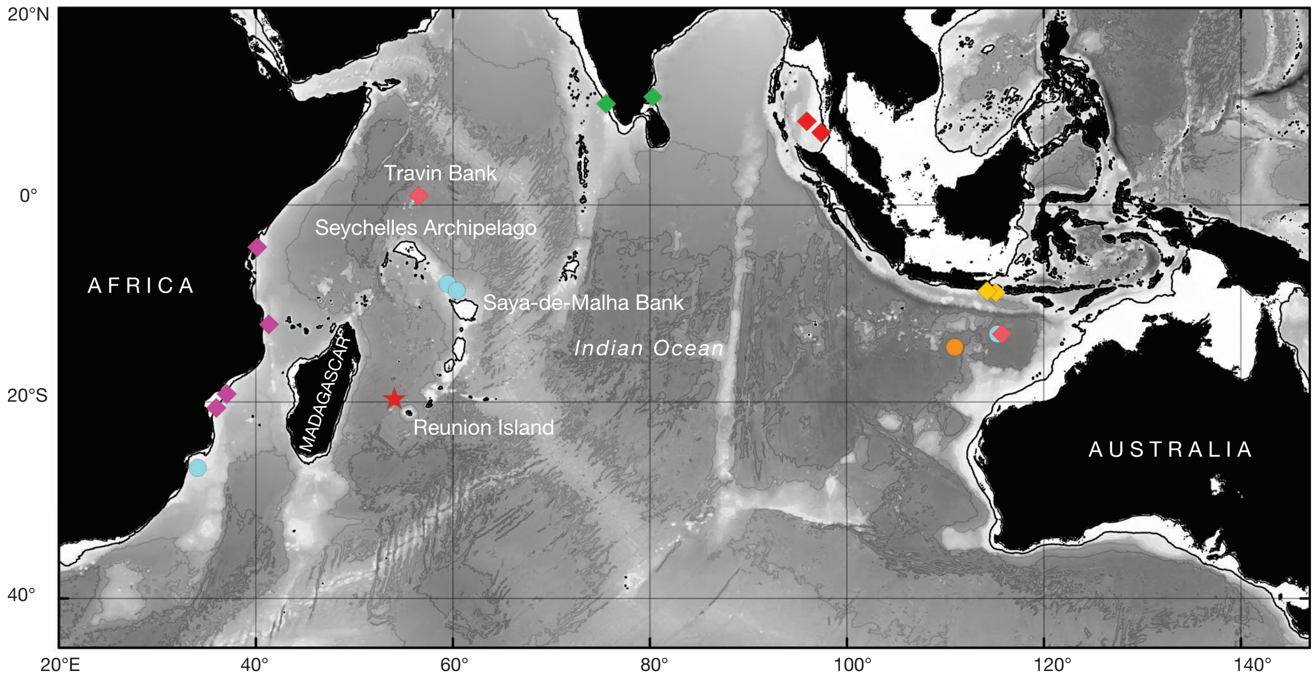

FIG. 1. — Geographic position of *Ectreposebastes* Garman, 1899 species records from the Indian Ocean. Symbols: *E. niger* (Fourmanoir, 1971): ★, this study; record of MNHN-IC-2019-0078; published records: ●, Mandrytsa (1990); ●, the specimen from the NSMT collection (Dr G. Shinohara, 2019 pers. comm.), also presented in GBIF (wrong position) and ALA 2017 (initial species identification as *E. imus* Garman, 1899 was modified by ALA team based on empirical criteria without examination of the specimen). *E. imus* Garman, 1899: Published records: ◆, specimens from YugNIRO cruises (collection ZISP) (Mandrytsa 1990); ◆, Indian records (Hashim 2012); ◆, from a Thailand survey (Kawai *et al.* 2017). Electronic references: ◆, SAIAB collection records (source: GBIF); ◆, from JETINDOFISH Project expeditions sampling stored both in NHMUK fish collection database and CAS (source; GBIF and NHMUK). Note that the occurrence positions of *E. niger* and *E. imus* in the Eastern Indian Ocean (Mandrytsa 1990) are artificially jittered to improve visibility and to decrease superposition, however, both individuals were caught in the same trawl. The 200 m isobaths (black line) and isobaths from 1000 to 5000 m (in 1000 m steps, light grey lines) are shown. Coastline and bathymetry data are from GEBCO (2003, 2016).

Straight length measurements were taken to the nearest mm with digital calipers following Eschmeyer & Collette (1966), Mandrytsa (1990), Kai & Nakabo (2013) and expressed as percentage of SL. Otoliths (Fig. 3) were examined under a light microscope (Olympus CX41 under × 40 magnification) and photographed with an Olympus E-5 digital camera, resolution 12 Mpx. Otolith description followed the terminology of Tuset *et al.* (2008). Most scales of the specimen were lost, therefore all scale counts correspond to the number of scale pockets.

GENETIC ANALYSIS

DNA was extracted in the laboratory from muscle tissue taken from the lower cranial area of the fish, close to the otoliths chambers. Tissue was air-dried, minced with a sterile scalpel on a Petri dish and incubated overnight in a Proteinase K and lysis buffer solution. The DNA extraction was completed using the NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's instructions.

The DNA-barcoding fragment of the mitochondrial cytochrome c oxidase subunit I gene (COI) was amplified using a primer cocktail (Ivanova *et al.* 2007). All amplifications were performed using illustra™ PuReTaq™ Ready-To-Go™ PCR Beads (GE Healthcare UK, Little Chalfont, UK) in a final volume of 25 µL containing 1 µL of each primer (10 pmol/µL) and 1-2 µL of genomic DNA.

The polymerase chain reaction (PCR) was set to an initial denaturation at 94°C for 5 min followed by 35 cycles of 30 s at 94°C, 40 s at 48°C and 50 s at 72°C with an additional final elongation phase of 7 min at 72°C.

The PCR product was checked via electrophoresis on a 1.5% agarose gel and product lengths were verified using a 100-1000 bp reference ladder. Ten microliters of PCR product were purified with a 2.5 µL mix containing exonuclease I (20 U/µL) and alkaline phosphatase (1 U/µL) using an incubation of 15 min at 37°C and 20 min at 75°C.

All purified PCR products were sequenced in both forward and reverse directions by Macrogen Inc. (Amsterdam, the Netherlands) using M13 universal primers.

Forward and reverse sequences were assembled using Geneious (v. R10, Biomatters, Auckland, NZ) and reciprocally verified, and a 555 bp long contig was generated. The sequence was then exported in FASTA format for further analysis. Sequence analysis was performed on Barcoding of Life Data System v. 4 (BOLD) (Ratnasingham & Hebert 2007) on 1 April 2019 using the Identification Engine, which searches in the entire BOLD reference database for best matches to the query sequence.

Phylogenetic and molecular evolutionary analyses were conducted using MEGA version X software (Kumar *et al.* 2018). The evolutionary history was inferred using the Neighbor-Joining method (Saitou & Nei 1987). The evolutionary distances were computed using the Maximum Composite Likelihood method (Tamura *et al.* 2004) with 1000 bootstraps using a species that evolved early in the Scorpaeniformes, *Trachyscorpia cristulata* (Goode & Bean, 1896), as an outgroup (an individual with BOLD ID ANGBF14113-19). Automatic Barcode Gap Discovery (ABGD) analysis (Puillandre *et al.* 2012) was applied to check potential species segregation within the genus *Ectreposebastes*, using online web interface available at https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html, consulted 10 August 2020.

Indian ocean limits

The Indian Ocean area is considered here following the official description of the International Hydrographic Organisation: from the Asian Continent to Antarctica, with its western and eastern borders positioned at 20°E off South Africa and 146°55'E off Southern Australia respectively (IHO 1953).

Abbreviations

Institutions, collectors (Sabaj 2019)

IRD	Institut de Recherche pour le Développement, Marseille;
MNHN	Muséum national d'Histoire naturelle, Paris;
NSMT	National Museum of Nature and Science, Tokyo.

Databases, programs

ALA	Atlas of Living Australia website at http://www.ala.org.au;
AFORO	A web-based environment for shape analysis of fish otoliths. http://aforo.cmima.csic.es/ (Lombarte *et al.* 2006);
FishBase	World Wide Web electronic publication. http://www.fishbase.org (Froese & Pauly 2019);
GBIF	Global Biodiversity Information Facility. http://data.gbif.org;
INSD	International Nucleotide Sequence Database. https://www.ddbj.nig.ac.jp/insdc-e.html, a joint database of INSDC, International Nucleotide Sequence Database Collaboration. http://www.insdc.org/;
NHMUK	Natural History Museum (2014). Dataset: Collection specimens. Resource: Specimens. Natural History Museum Data Portal (data.nhm.ac.uk). https://doi.org/10.5519/0002965, http://data.nhm.ac.uk/;
OBIS	The Ocean Biogeographic Information System. https://obis.org/;
SAIAB fish	South African Institute for Aquatic Biodiversity fish collection database of the South Africa http://specify-portal.saiab.ac.za/specify-solr/fish/ as on 19.01.2017, currently https://www.gbif.org/dataset/1aaec653-c71c-4695-9b6e-0e26214dd817, accessed 22 July 2020;
WoRMS	World Register of Marine Species http://www.marinespecies.org.

Measurements and counts

LL	lateral line;
OL	otolith length;
OH	otolith height;
SL	standard length;
TL	total length.

SYSTEMATIC ACCOUNT

Family Setarchidae Matsubara, 1943
Genus *Ectreposebastes* Garman, 1899

Ectreposebastes niger (Fourmanoir, 1971)
(Fig. 2)

Pontinus niger Fourmanoir, 1971: 42, fig. 6.

Type material. — **Holotype. Pacific Ocean** • MNHN-IC-1970-0034, 122 mm SL, 09°56'S, 141°52'W; 0-1200 m depth; 12.IX.1969; CARIDE 5; R/V *Coriolis*.

Material examined. — **La Réunion** • MNHN-IC-2019-0078; no sex data; 165 mm SL; Southwestern Indian Ocean; 19°45.84'S, 54°05.28'E-19°41.43'S, 54°03.80'E; 18.IX.2016; Romanov, IRD LA PÉROUSE leg; R/V *Antea*.

Distribution. — Indo-West Pacific meso- and bathy-pelagic, mostly near continental/peri-insular slopes in tropical and temperate waters.

Description

Individual MNHN-IC-2019-0078 (165 mm SL)

External morphology. Medium-sized, black-coloured scorpaeniform fish with black-yellowish eyes. Pinkish muscles visible through semi-transparent skin in scale pockets; scale pocket edges black. Body relatively high, slightly compressed laterally, flabby, lacking scales (most scales lost, except some pored LL scales) (Fig. 2). Most fin spines, some fin rays broken due to fragile, poorly-ossified nature. First pre-opercular spine weakly developed; others damaged. Lacrimal spines short, intact on the left side but damaged on right. Body proportions shown in Table 1.

Otoliths. Thick and robust. Otolith shape triangular with pointed rostrum (Fig. 3); ventral rim convex; post-dorsal rim almost straight without depression; pre-dorsal rim forming angle close to 90° with post-dorsal rim. Otolith height almost equal to otolith length (ratio OH/OL 0.75-0.79 for right and left otoliths respectively). *Sulcus acusticus*: archaesulcoid, ostial, median. *Ostium* and *cauda*: undifferentiated, oval. Anterior region: double-peaked; rostrum broad, short, slightly pointed, antirostrum very short, rounded, broad; *excisura* wide with shallow notch. Posterior region: oblique to round or oblique to irregular.

Remark

The morphology of our specimen corresponds well to the original description given by Fourmanoir (1971) and later by Mandrytsa (1990). Body measurements are close to the ranges presented in other studies. However, many proportions are close to or even outside of the lower end of reported ranges (Table 1).

Genetic analysis

A 555 bp region of the mtDNA COI gene was isolated from the specimen and the sequence was deposited in the INSD (accession number: MN181524). The query sequence did not find 100% match to the mtDNA COI region of any other

Fig. 2. — Individual of *Ectreposebastes niger* (Fourmanoir, 1971) caught in the pelagic environment during the LA PÉROUSE cruise. Scale bar: 10 mm. Specimen MNHN-IC-2019-0078. Photo credit: Francis Marsac.

specimens. The nearest matches were non-identified specimens *Ectreposebastes* sp. (98.13% to 98.31% similarity) and *Ectreposebastes imus* (97.10% to 98.13% similarity). Neighbour joining tree analysis (Fig. 6) shows distinct clustering between *E. imus*, *E. niger* and *Ectreposebastes* sp. DNA signatures. The *E. imus* branch is separated from another branch that contains our *E. niger* specimen (MN181524) and *Ectreposebastes* sp. specimens (FOAE60706, FOAF803-07) collected from the Southwestern Pacific: Coral Sea (off Australian coast) and from over Lord Howe Rise.

An ABGD analysis aimed at detecting genetic gaps between species (Puillandre *et al.* 2012) clustered *Ectreposebastes* sequences into three lineages, segregating *E. imus*, *E. niger* (MN181524) and *Ectreposebastes* sp.

DISCUSSION

Morphology, genetics, identification

Morphology and meristic counts of *E. niger* presented here correspond well to other individuals of this species reported in the literature (Table 1). Our specimen is the largest individual of *E. niger* ever reported globally (Fourmanoir 1971; Paulin 1982; Mandrytsa 1990). Hence, values of body proportions, which are close to or beyond the lower reported range, may represent individual growth-related variability.

Externally, our specimen differs from the congeneric *E. imus* by having larger and fewer scales: lower number of horizontal rows of scales above (8 vs 14-16) and below (25 vs 35-48) the LL and lower total number of vertical scale rows (54 vs 83-95) (Mandrytsa 1990). The number of predorsal scales in our individual (11) exceeds the number of predorsal scales observed earlier in *E. niger* (8-10), but does not overlap with *E. imus* (12-17) (Table 1). It appears that *E. niger* also has shorter pelvic fins and a higher caudal peduncle than *E. imus* (Table 1). Other interspecific differences mentioned in Mandrytsa (1990) (such as longer dorsal fin base and body height) are highly variable among different individuals (Table 1), often overlapping between species, and cannot be used as identification characters. Length of lacrimal and preopercular spines also cannot be used in many cases as the spines are often broken due to their fragile nature. Apparently, scale size and counts are the sole external indicators that allow intrageneric morphological identification of *Ectreposebastes* species.

Genetic analysis shows that the level of segregation between *Ectreposebastes* species is very low. Evolutionary distance between the sequence of our specimen (MN181524) and reference sequences of *E. imus* ranged within 0.0190-0.0248, while distance with *Ectreposebastes* sp. lies between 0.0170-0.0190. However, distinct clustering detected through neighbour joining tree analysis (Fig. 6) indicated segregation of *E. imus* from *E. niger* and *Ectreposebastes* sp. ABGD analysis confirms that *E. imus* and *E. niger* (MN181524) are separate species. At the same time ABGD shows that *Ectreposebastes* sp. from the Southwestern Pacific and *E. niger* (MN181524) represents separate linages. Considering that the *E. niger* holotype originated from the southern Pacific (French Polynesia), the two individuals of *Ectreposebastes* sp. (FOAE60706, FOAF803-07) collected in the Coral Sea may represent the 'true' *E. niger*. The genetic divergence of the Indian Ocean lineage identified here as *E. niger* (MN181524) based on morphological criteria may indicate ongoing allopatric speciation between Pacific and Indian Ocean populations. Further studies are necessary to better understand the level of divergence within *E. niger* across the Indo-Pacific, and therefore genetic sampling, careful examination and preservation are essential for any specimens discovered in the future.

The separation of *E. niger* and *E. imus* remains challenging in view of their overall morphological and genetic similarity. For example, the synonymisation of the two species by

TABLE 1. — Total length and body proportions (in % of SL, except TL, SL, otoliths length and height in mm, total weight and otoliths weight in g) of *Ectreposebastes niger* (Fourmanoir, 1971) from the south-western Indian Ocean and from specimens collected in the Indian Ocean and the Pacific. Comparative measurements for *E. imus* Garman, 1899 are also given. Measured dimensions are given following terminology of Mandrytsa (1990) and Kai & Nakabo (2013), except for terms and measurements adopted from Escánez & Brito (2011) given in *italics*, and from Frable *et al.* 2015 given in ***bold italics***. Non-overlapping characters between the two species are underlined. * Including 3 ind. from Scherbachev *et al.* 1978 (measurements and proportions are taken from Mandrytsa (1990)).

	***Ectreposebastes niger* (Fourmanoir, 1971)**				***E. imus* Garman, 1899**		
Measurement	**This study, MNHN-IC-2019-0078**	**holotype MNHN-IC-1970-34**	**Scherbachev *et al.* (1978)**	**Mandrytsa (1990)**	**Mandrytsa (1990)**	**Eschmeyer & Collette (1966)**	**Escánez & Brito (2011)**
n	1	1	3	7*	8	37	2
Total length	183	–	–	–	–	–	84, 98
Standard length	165	118	90, 120, 125	112.7 (83.0-141.5)	136.9 (55.0-222.0)	–	71, 83
Snout length	12.7	13.2	14.6, 14.2, 14.1	12.5 (11.4-13.6)	13.2 (11.5-15.1)	14.2 (13.0-17.0)	14.1, 12.0
Orbit diameter horizontal	4.9	7.4	6.4, 7.1, 6.9	7.7 (6.8-8.5)	7.6 (6.0-9.2)	–	7.0, 8.4
Head length	34.7	38.2	44.5, 40.6, 41.4	41.0 (38.5-42.9)	41.5 (38.6-44.1)	–	39.4, 45.8
Interorbital width	12.5	13.5	13.2, 12.8, 13.1	12.6 (10.8-13.7)	12.6 (11.4-14.2)	12.9 (10.0-15.0)	–
Upper jaw length	23.2	23.4	25.5, 24.6, 25.1	25.3 (24.6-25.9)	24.1 (20.4-26.4)	–	–
Predorsal fin length	34.0	38.5	39.4, 39.5, 39.4	36.4 (34.9-38.6)	38.3 (30.5-43.3)	45.8 (41.0-49.0)	–
Preanal fin length	71.9	77.0	–	69.5 (67.4-75.0)	70.6 (64.4-76.1)	–	–
Prepectoral fin length	41.8	44.7	–	42.6 (40.1-43.7)	43.5 (39.2-47.2)	–	–
Prepelvic fin length	*45.5*	–	–	–	–	–	–
Body depth (max)	39.1	38.1	35.7, 32.3, 33.4	31.8 (28.6-36.1)	38.7 (31.9-49.6)	42.3 (37.0-52.0)	43.7, 41.0
Depth at dorsal fin origin	***37.4***	–	–	–	–	–	–
Depth at pelvic fin origin	***37.5***	–	–	–	–	–	–
Depth at anal fin origin	***33.6***	–	–	–	–	–	–
Caudal peduncle depth	13.5	11.0	–	9.5 (8.6-10.0)	9.0 (8.0-9.6)	–	8.5, 8.4
Length of dorsal fin base	54.6	50.4	–	54.8 (50.5-57.4)	51.7 (49.2-59.1)	–	–
Spinous dorsal fin base length	***39.6***	–	–	–	–	–	–
Soft rayed dorsal fin base length	***18.1***	–	–	–	–	–	–
1st dorsal fin spine length	1.2	4.1	–	6.3 (5.1-7.3)	7.0 (6.6-7.2)	–	–
2nd dorsal fin spine length	1.7	–	–	10.6	10.6 (9.9-11.3)	–	–
3rd dorsal fin spine length	3.9	–	–	–	–	–	–
4th dorsal fin spine length	3.1	–	–	–	–	–	–
5th dorsal fin spine length	4.0	–	–	–	–	–	–
Pectoral fin length	34.8	44.7	40.0, 35.0, 35.2	38.2 (35.3-40.7)	39.7 (32.3-43.6)	–	38.0, 38.6
Pectoral fin base depth	***11.9***	–	–	–	–	–	–
Pelvic fin ray length	<u>9.4</u>	<u>18.8</u>	–	<u>18.2 (18.2)</u>	<u>23.4 (22.0-26.4)</u>	–	–
Pelvic fin spine length	5.1	–	–	–	–	–	–

Table 1. — Continuation.

	Ectreposebastes niger (Fournanoir, 1971)				*E. imus* Garman, 1899		
Measurement	**This study, MNHN-IC-2019-0078**	**holotype MNHN-IC-1970-34**	**Scherbachev *et al.* (1978)**	**Mandrytsa (1990)**	**Mandrytsa (1990)**	**Eschmeyer & Collette (1966)**	**Escánez & Brito (2011)**
Anal fin base length	16.0	15.9	–	16.1 (15.4-17.6)	14.4 (13.5-15.6)	–	–
Anal fin spine I length	2.4	–	–	3.7 (2.9-4.5)	3.6 (2.7-4.1)	–	–
Anal fin spine II length	7.9	–	–	6.7 (5.8-7.7)	8.7 (6.6-10.9)	–	–
Anal fin spine III length	4.5	–	–	9.0 (8.4-9.6)	10.8 (9.0-12.7)	–	–
Caudal peduncle dorsal length	8.1	–	–	–	–	–	–
Caudal peduncle ventral length	12.6	16.1*	–	17.6 (15.5-18.7)*	15.8 (13.9-18.4)	–	–
Length of 1st lacrimal spine	0.8	0.8	–	1.7 (1.3-2.0)	1.4 (0.9-2.0)	–	–
Length of 2nd lacrimal spine	1.1	0.8	–	1.6 (1.1-2.0)	1.3 (1.0-2.9)	–	–
Length of 1st preopercular spine	2.6	1.3	–	4.1 (3.6-4.5)	5.0 (3.6-5.8)	–	–
Length of 2nd preopercular spine	damaged	1.9	–	5.1 (3.9-6.1)	6.1 (3.9-10.0)	–	–
Length of 3rd preopercular spine	damaged	2.5	–	6.1 (5.9-6.3)	7.3 (5.6-9.6)	–	–
No. dorsal spines	12	12	12	12	–	12	12
No. dorsal soft rays	10	10	10	10 (9)	–	9-10	9
No. anal spines	3	3	3	3	–	3	3
No. anal soft rays	6	6	6	6	–	5-6	6
No. pectoral rays	18	16	18-19	18 (16-19)	–	18-20	18, 16
No. caudal rays	*27*	–	–	–	–	–	*20, 20*
No scales on lateral line	25	32	27-28	27-28	–	–	–
Scales above LL at mid dorsal fin spiny part	8	–	7	8-10	14-16	–	10, 13
Scales below LL at mid dorsal fin spiny part	25	–	19-23	22-32	35-48	–	29, 30
Vertical scale raws	54	55	–	55-63	83-95	–	–
Predorsal scales	11	–	9-10	8-10	12-17	–	–
Gillrakers on 1 arch	14 (Upper 6, Lower 8)	–	–	15-18 (5-7+1+8-10)	–	–	–
Otolith length (L/R)	3.94 / 3.83	–	–	–	–	–	–
Otolith height (L/R)	2.95 / 3.04	–	–	–	–	–	–
Otolith weight (L/R)	0.0097 / 0.0096	–	–	–	–	–	–
Total weight after defrosting	142.7	–	–	–	–	–	–

Collette & Uyeno (1972) was apparently based on misidentification. The individual (NSMT-P 17480) described by Collette & Uyeno (1972) is obviously distinct from *E. niger* by its smaller scales (12 above LL and 35-38 below LL) representing, therefore, *E. imus*.

The number of pored scales in the LL of *Ectreposebastes* spp. is an uncertain character. Combined information from available *E. niger* descriptions given by Fourmanoir (1971), Scherbachev *et al.* (1978), Mandrytsa (1990) and the present study, suggests 25-32 pored LL scales (Table 1). Most descriptions of *E. imus* are lacking information on the number of LL scales, however, Collette & Uyeno (1972) reported *c.* 45 pored scales in the LL of their specimen. Photographs presented in various papers (Eschmeyer & Randall 1975; Maruyama & Ono 1975; González *et al.* 2014) and photos of museum collection specimens stored in SAIAB (catalogue number 82172) and MCZ (catalogue numbers 164078 and 163321) (accessed through GBIF 2020), demonstrate a much lower number of scales in the LL than mentioned by Collette & Uyeno (1972), close to the range of *E. niger*.

Otolith shape in teleosts tends to be highly species-specific and is widely used in species identification (Jobling & Breiby 1986; Smale *et al.* 1995; Granadeiro & Silva 2000; Campana 2004, 2005). Here we present the first descrip-

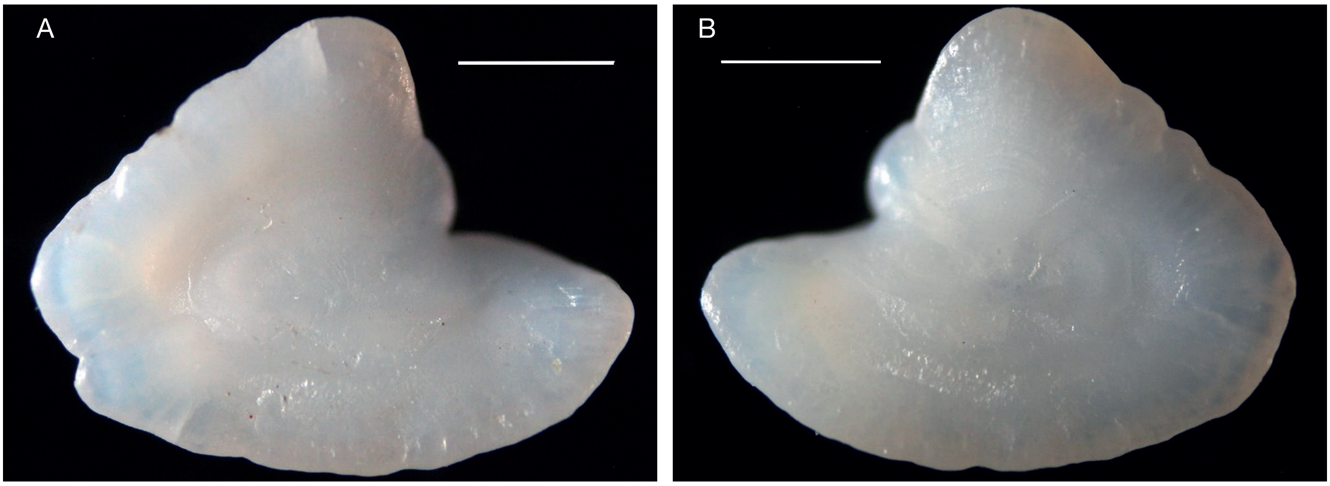

Fig. 3. — Otoliths: left (**A**), right (**B**) of *Ectreposebastes niger* (Fourmanoir, 1971), 165 mm SL, 183 mm TL, reported in this study. MNHN-IC-2019-0078. Scale bars: 1 mm.

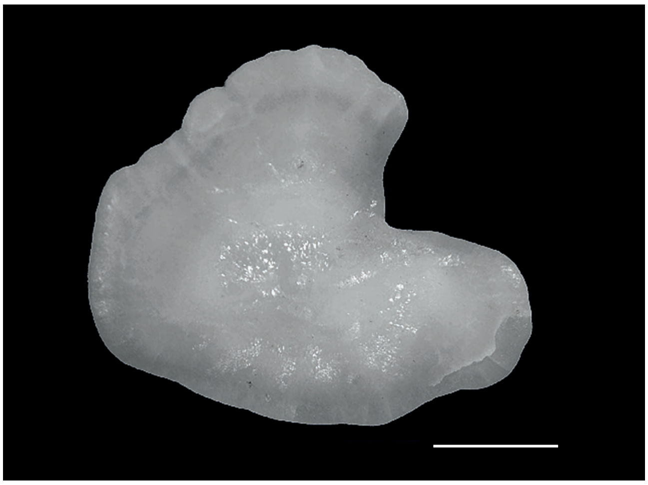

Fig. 4. — Left otolith of *Ectreposebastes imus* Garman, 1899 (160 mm total length) from Belize, Caribbean Sea, Western Atlantic. Scale bar: 1 mm. Source: AFORO, Fish ID: 9300.

tion of otolith shape of *E. niger* and comparison with its congener *E. imus*. Otolith OH/OL ratio and overall shape are similar for both species (Figs 3-5). Nevertheless, the otoliths of *E. niger* are clearly distinct from those of *E. imus* of similar sizes. Otoliths of *E. niger* reported in this study had a slightly pointed rostrum and short, rounded antirostrum (Figs 3; 5). In contrast, otoliths of *E. imus* from specimens > 90 mm FL presented in Campana (2004) and the AFORO database (Lombarte *et al.* 2006) demonstrate a rounded rostrum while the antirostrum was either lacking (Campana 2004) or bluntly pointed (Figs 4; 5). The otolith contour of *E. imus* is less 'angular' than that of *E. niger*. Visible differences in otolith shape between *Ectreposebastes* species suggest that this may be an additional robust morphological diagnostic feature. Otolith shape analysis of Pacific *E. niger* specimens may provide further indicators (besides genetics) on potential divergence from the putative Indian Ocean population.

Distribution in the Indian Ocean

To date, seven individuals of *E. niger* have been reported in the literature from the Indian Ocean region (Table 2). The first records were described by Scherbachev *et al.* (1978), who reported three individuals caught by midwater and bottom trawls during Soviet research cruises in the Mozambique Channel and over the Saya-de-Malha Bank (Fig. 1). Scherbachev *et al.* (1978) identified them as *Ectreposebastes* sp. (mentioning however differences with *E. imus*) while re-examination by Mandrytsa (1990) finally attributed these individuals to *E. niger*. Another four individuals were caught, also by the USSR vessels, at the Saya-de-Malha Bank and off Java in 1976-1982, using bottom and midwater trawls respectively (Mandrytsa 1990) (Fig. 1), (Table 2). No new records in the region were reported since.

Direct correspondence with museums allowed us, however, to obtain data on another *E. niger* individual collected from the Indian Ocean. The specimen stored in National Museum of Nature and Science, Tokyo, initially identified as *E. imus* (NSMT-P 61091) was found in the stomach of a longnose lancetfish *Alepisaurus ferox* Lowe, 1833 caught in the open Eastern Indian Ocean in 1982 by tuna longline at approximately 170 m depth (Fig. 1; Table 2). Based on scale counts of the preserved specimen (9 horizontal rows above and 34 below LL) and a photograph (G. Shinohara, 2019, pers. comm.) we identified the specimen NSMT-P 61091 as *E. niger*.

Our record (MNHN-IC-2019-0078) represents the first occurrence of this pelagic scorpionfish in the waters of Reunion Island (Fricke 1999; Letourneur *et al.* 2004; Fricke *et al.* 2009) confirming the presence of this species along the Mascarene Ridge: from Saya-de-Malha Bank (past records) to Reunion Island (this study).

Besides the Indian Ocean, *E. niger* occurrence was documented in the Western and Central Pacific Ocean (Fourmanoir 1971; Paulin 1982; ALA 2017); however, no individual was recorded to date in the Eastern Pacific.

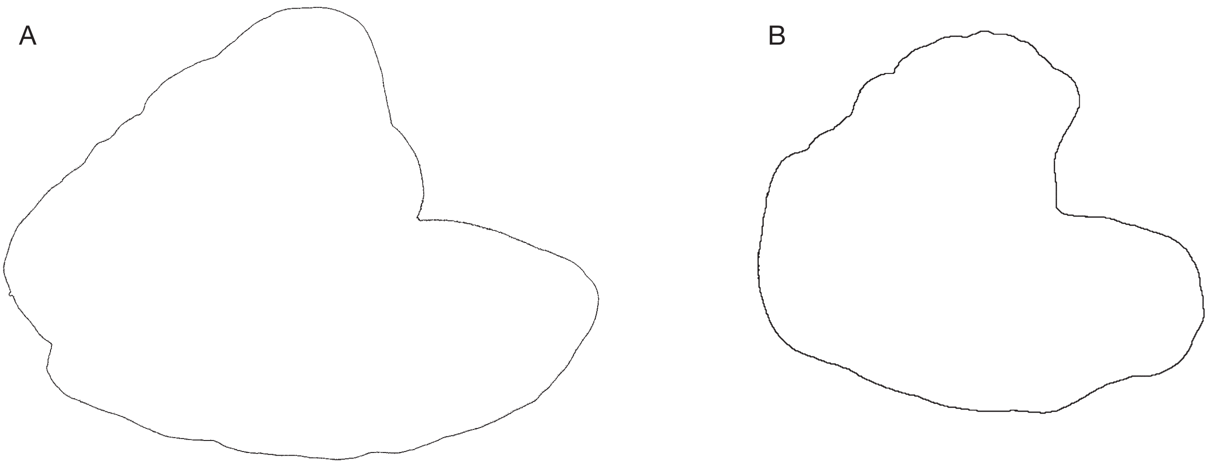

Fig. 5. — Contours of left otoliths of *Ectreposebastes* Garman, 1899 showing difference in otolith shape between the two species of the genus: **A**, *Ectreposebastes niger* (Fourmanoir, 1971) (this study MNHN-IC-2019-0078); **B**, *Ectreposebastes imus* Garman, 1899 from Belize, Caribbean Sea, Western Atlantic. Source: AFORO, Fish ID: 9300.

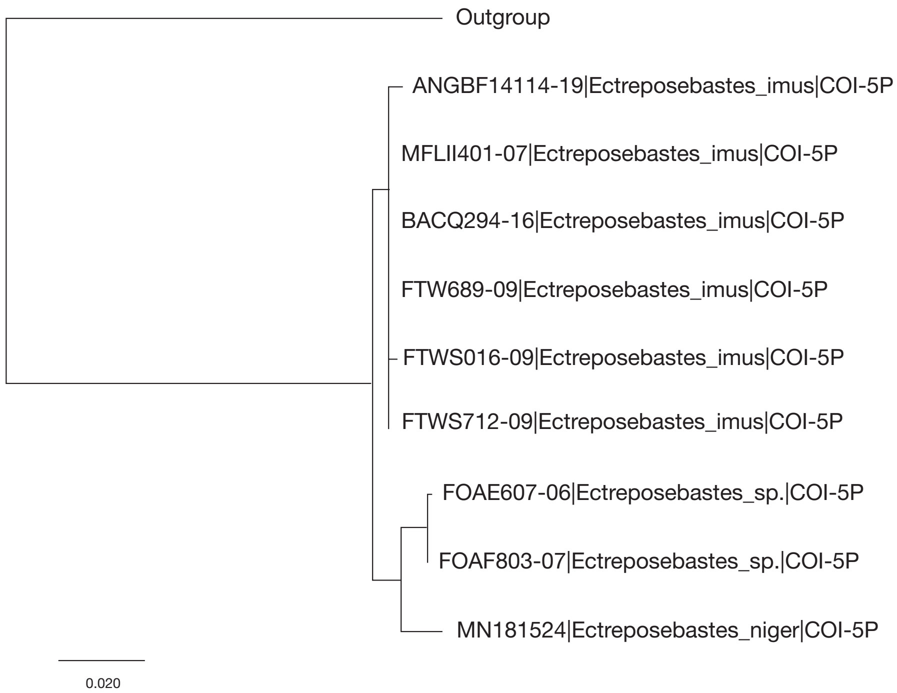

Fig. 6. — Neighbour joining tree of the genus *Ectreposebastes* Garman, 1899 based on DNA sequences of the mitochondrial COI gene. The tree was constructed based on *Ectreposebastes* spp. sequences publicly available in Barcoding of Life Data System v. 4 (BOLD) and the sequence from our specimen of *Ectreposebastes niger* (Fourmanoir, 1971) (MNHN-IC-2019-0078, BOLD accession number: MN181524). The optimal tree with the sum of branch length = 0.22318084 is shown. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. *Trachyscorpia cristulata* (Goode & Bean, 1896) (BOLD ID ANGBF14113-19) were used as outgroup.

Occurrences of the congeneric *E. imus* are widely reported throughout the Indian Ocean from the Mozambique Channel, Kenya and in the vicinity of the Travin Bank (00°26'N, 56°00'E) in the west, through India and the Bay of Bengal to Indonesia in the east (Mandrytsa 1990; Pauly *et al.* 1996; Hashim 2012; Govindam *et al.* 2013).

Before this study, the most recent specimen of the genus *Ectreposebastes* recorded in the south-western Indian Ocean was an individual collected during the pelagic ecosystem survey in Mauritius and the Southern Mascarene region by the R/V *Dr. Fridtjof Nansen* (Strømme *et al.* 2010). However, the specimen was not identified to species level and it was

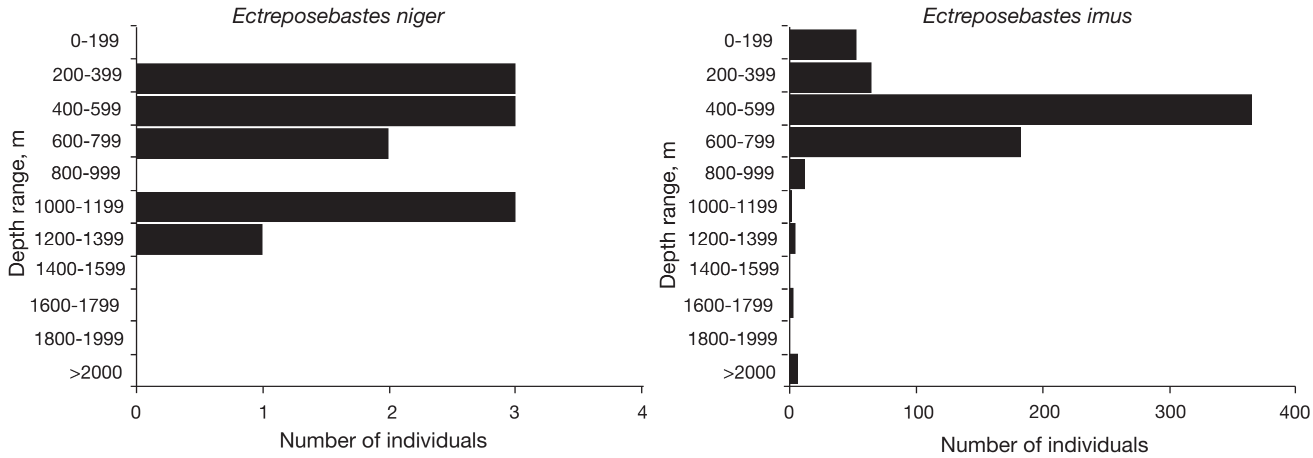

Fig. 7. — Global bathymetric distribution (all records with known capture depth) of *Ectreposebastes niger* (Fourmanoir, 1971) (n = 12) (left panel) and *Ectreposebastes imus* Garman, 1899 (n = 698) (right panel). Data sources are listed in Table 2 and also in Eschmeyer & Collette (1966); Eschmeyer (1969); Collette & Uyeno (1972); Eschmeyer & Randall (1975); Maruyama & Ono (1975); Paulin (1982); Badrudin *et al.* (2007); Balanov *et al.* (2009); De Paiva *et al.* (2011); Escánez & Brito (2011); González *et al.* (2014); Chung (2015); ALA, accessed 19 January 2017; GBIF, accessed 19 January 2017; OBIS, accessed 22 July 2020; NHMUK accessed 19 January 2017. The single record of *E. niger* at the depth of 170 m, which was recovered from a predator's stomach (*Alepisaurus ferox*) is not considered here.

not possible to locate the specimen or to obtain a copy of the final version of the report.

Non-georeferenced sources also indicate the presence of *Ectreposebastes* species off Indonesia (Pauly *et al.* 1996; Badrudin *et al.* 2007) and along the south-west coast of India (Govindam *et al.* 2013; Venu 2013).

Online databases (OBIS, GBIF) referenced to museum collections (e.g. SAIAB, CSIRO, MCZ) and published records (Eschmeyer 1969; Eschmeyer & Collette 1966; Maruyama & Ono 1975; Balanov *et al.* 2009; De Paiva *et al.* 2011; Escánez & Brito 2011; Gonzáles *et al.* 2014; Tatsuta *et al.* 2014, Motomura & Struthers 2015) confirm the wide occurrence of *E. imus* (GBIF 2017, 2020; OBIS 2017, 2020) suggesting its circumglobal distribution. Outside the Indian Ocean (Fig. 1) its records spread across the Atlantic, while Pacific occurrences are patchy, mostly in the North and Equatorial Western Pacific, Hawaiian Islands (Central Subtropical Pacific), Galápagos Islands (Eastern Central Pacific) and continental slope of Ecuador and Peru.

It should be mentioned, however, that online databases are always a source of ambiguity in species distributions and taxonomy (Romanov *et al.* 2013). Online database sources, e.g. *Catalog of Fishes* (currently *Eschmeyer's Catalog of Fishes*) (Eschmeyer & Fricke 2012; Fricke *et al.* 2020), GBIF, OBIS, SAIAB search portal and ALA are evolving rapidly with changing content, cross-links and URLs. Therefore the use of online databases in their current form without stable URLs and backward content traceability is prone to uncertainty. Their use as a reference and source of data in taxonomic papers is challenging.

A further source of uncertainty in online resources results from several museum specimens that were collected and identified during the period of synonymisation of the two species (CAS, NHMUK): no signs of re-examination are available yet.

Habitat

Our results and the available published information suggest that *Ectreposebastes* species are distributed along continental/peri-insular shelves, in proximity to seamounts and apparently in deep open-ocean pelagic habitat.

Globally, both species of *Ectreposebastes* occur in the midwater layer far from the bottom, while catches with demersal trawls (Table 2) and ROV observations on the bottom are also reported (Robertson & Van Tassell 2019). A summary of distribution occurrences by depth strata (Fig. 7) demonstrates that the habitat of the pelagic scorpionfish, *E. niger*, ranged from the upper mesopelagic layer (below 200 m depth) to the bathypelagic depths 1200-1300 m (Mandrytsa 1990). The midwater scorpionfish, *E. imus*, occurs in the epipelagic zone (shallower than 200 m) reaching depths of at least 1000-1150 m according to published records (Collette & Uyeno 1972; Grove & Lavenberg 1997; Badrudin *et al.* 2007). While most sources (e.g. Eschmeyer 1969) suggest 500-800 m depth as preferred habitat for *E. imus*, our compilation (GBIF 2020; OBIS 2020) demonstrates a wider range, through the entire meso- and bathypelagic zones (Fig. 7).

Most *Ectreposebastes* occurrences are associated with seamounts (e.g. La Pérouse seamount (this study); Travin Bank, and Saya-de-Malha Bank) or continental slope areas (Fig. 1; Table 2) (Mandrytsa 1990). In Hawaiian waters, *E. imus* was classified as a potential member of the mesopelagic-boundary community (Reid *et al.* 1991) and called a 'pseudo-oceanic species' (Hulley & Lutjeharms 1989), i.e., inhabiting the mesopelagic-boundary zone that 'overlies the depths where mesopelagic waters impinge on the upper slope of a land mass, island or seamount'.

However, the pelagic scorpionfish reported in the present study was caught in the mesopelagic zone together with 'high-oceanic fishes' like *Benthosema suborbitale* (Gilbert, 1913), *Ceratoscopelus warmingii* (Lütken, 1892), *Sigmops elongatus*

TABLE 2. — Details of capture positions of the Indian Ocean *Ectreposebastes* spp. presented in Fig. 1. Non geo-referenced occurrences are not mapped and not given here. Abbreviations: **TRAWB**, bottom trawl; **TRAWBO**, otter trawl; **TRAWP** pelagic (midwater) trawl; **LLP**, pelagic longline; **ALX**, lancetfish *Alepisaurus ferox* Lowe, 1833; **SL**, standard length; **N/A**, non-available. Geographic positions presented in decimal form in the source were converted into dd°mm.m format. * Re-examined and identified as *E. niger* (Fourmanoir, 1971) by Mandrytsa (1990); ** Apparently collected together. JETINDOFISH Trawl Survey operated in the Indian Ocean (Lohmeyer 1996).

Capture date	Latitude (dd°mm.m)	Longitude (ddd°mm.m)	Sampling gear	Species as given in the source	Collector / Museum	Capture depth, m	Catalogue number	SL	No.	Vessel	Source
Ectreposebastes niger (Fourmanoir, 1971)											
Published data											
27.09.1973	26°41.0' S	034°06.0' E	TRAWB	*E. sp.**	- / ZISP	1000	49421	90	1	R/V Fiolent	Scherbachev *et al.* 1978
18.06.1976	08°42.0' S	060°23.0' E	TRAWP	*E. sp.**	- / ZISP	658-722	49422	120, 125	2	R/V Zvezda Kryma	Scherbachev *et al.* 1978
09.11.1976	08°00.0' S	059°28.0' E	TRAWB	*E. niger*	- / ZMMU	1200-1320	P-18044	134.5	1	R/V Zvezda Kryma	Mandrytsa 1990
26.04.1982	13°06.0' S	115°31.0' E	TRAWP	*E. niger*	- / ZISP	390-425	49423	83-141.5	3	R/V Fiolent	Mandrytsa 1990
Museum collections – direct correspondence											
12.01.1982	14°26.0' S	110°52.9' E	LLP, stomach of ALX	*E. imus*	NSMT	170	NSMT-P 61091	127.0	1	Syonan-maru	Dr. G. Shinohara 2019 pers. comm.
This study											
18.09.2016	19°41.43' – 19°45.84' S	054°03.80' – 054°05.28' E	TRAWP	*E. niger*	EVR, YC, FM / MNHN	475-560	MNHN-IC-2019-0078	165	1	R/V Antea	LA PÉROUSE cruise, IRD, 2016
Ectreposebastes imus Garman, 1899											
Published data											
16.06.1976	00°57.0' N	056°32.0' E	TRAWP	*E. imus*	- / ZISP	800-820	49437	191	1	R/V Zvezda Kryma	Mandrytsa 1990
26.04.1982	13°06.0' S	115°31.0' E	TRAWP	*E. imus*	- / ZISP	390-425	49438	55	1	R/V Fiolent	Mandrytsa 1990
N/A	10°16.0' N;	075°33.0' E	TRAWBO	*E. imus*	–	777	–	–	N/A	FORV Sagar Sampada	Hashim 2012
N/A	10°58.0' N;	080°19.0' E	TRAWBO	*E. imus*	–	637	–	–	N/A	FORV Sagar Sampada	Hashim 2012
27.01.1999	07°21.0'- 07°20.0' N	097°26.0'- 097°25.0' E	TRAWBO	*E. imus*	PMBC	520–531	PMBC 27953	108.9	1	R/V Chakratong Tongyai	Kawai *et al.* 2017
05.02.1999	08°30.0' - 08°28.0' N	095°58.0'- 095°58.0' E	TRAWBO	*E. imus*	PMBC	649–550	PMBC 27954	78.2	1	R/V Chakratong Tongyai	Kawai *et al.* 2017
Online sources											
15.07.1979**	08°45.08' S	114°16.00' E	TRAWP	*E. imus*	JETINDOFISH Trawl Survey / CAS	40-180	CAS 54557, CAS 54558	–	2	Jurong	ALA 2018 / NHMUK 2014
15.07.1979**	08°45.08' S	114°16.00' E	TRAWP	*E. imus*	JETINDOFISH Trawl Survey / NHMUK	–	1986.11.27.58-62	–	1	Jurong	NHMUK 2014
1979-1983	08°43.00' S	114°15.00' E	TRAWP	*E. imus*	JETINDOFISH Trawl Survey / NHMUK	–	1984.1.1.63	–	1	Jurong	NHMUK 2014
16.07.1979	08°54.00' S	115°09.00' E	TRAWP	*E. imus*	JETINDOFISH Trawl Survey / NHMUK	–	1986.11.27.55	–	1	Jurong	NHMUK 2014
16.07.1979	08°54.00' S	115°09.00' E	TRAWP	*E. imus*	JETINDOFISH Trawl Survey / NHMUK	–	1986.11.27.56-57	–	1	Jurong	NHMUK 2014
10.12.1980	04°17.0' S	040°07.0' E	–	*E. imus*	SAIAB	687-750	14035	–	1	–	SAIAB 2017
19.10.2007	20°35.6' S	035°58.3' E	TRAWB	*E. imus*	SAIAB	709-721	82172	76	1	–	SAIAB 2017
24.10.2007	19°10.9' S	037°02.2' E	TRAWB	*E. imus*	SAIAB	444-453	82367	46	1	–	SAIAB 2017
18.11.2007	12°06.0' S	041°18.0' E	TRAWP	*E. imus*	SAIAB	510	66019	–	1	–	SAIAB 2017

(Günther, 1878), *Argyropelecus aculeatus* Valenciennes, 1850, *Argyropelecus hemigymnus* Cocco, 1829, and other high-oceanic species from families Evermannellidae Fowler, 1901 and Melamphaidae Gill, 1893 (Cherel *et al.* 2020). Indeed, several records of adults, juveniles and larvae (Moser *et al.* 1977) from pelagic environments show the rather ubiquitous distribution of *Ectreposebastes* species in the mesopelagic zone of the open ocean.

Alternatively these pelagic records may represent 'lost' individuals transported into oceanic environments by ocean currents. The body shape of *Ectreposebastes* spp. suggests that both species are not strong swimmers; apparently they are not capable of counteracting a persistent current flow. This renders them vulnerable to predators well adapted to pelagic environment. At least two records of *E. imus* and one of *E. niger* were reported from stomachs of the longnose lancetfish *Alepisaurus ferox* (Moser *et al.* 1977; Choy *et al.* 2013 Suppl.; Shinohara 2019, pers. comm.), which is known as an ambush pelagic predator (Romanov & Zamorov 2002) inhabiting epi- and mesopelagic layers worldwide.

Acknowledgements

We are thankful to the captain and the crew of the R/V *Antea* for their contribution in fishing operations and overall assistance during the research cruise. The laboratory 'biome-id' (Germany) performed DNA barcoding. Dr Gento Shinohara, National Museum of Nature and Science, Japan provided a photograph, scale counts and capture-associated information on the *Ectreposebastes* specimen from the NSMT collections. Natalya Romanova helped in data compilation on *Ectreposebastes* bathymetric distribution. The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure. We appreciate assistance with the English of the manuscript provided by Dr R. Charles Anderson. Two anonymous referees provided valuable suggestions that expand this paper scope and improved its content.

REFERENCES

Allen G. R., Hoese D. F., Cross N. J. & Bray D. J. 2006. — Sebastidae, Setarchidae, Neosebastidae, Tetratogidae, Synanceiidae, Anthiinae, *in* Beesley P. & Wells A. (eds), *Zoological Catalogue of Australia*. Volume 35. Fishes. Pt. 2. CSIRO Publishing, Canberra: 866-997.

ALA 2017. — Atlas of Living Australia website. http://biocache.ala.org.au/occurrences/search?&q=raw_taxon_name%3A%22Ectreposebastes+imus%22+OR+raw_taxon_name%3A%22Ectreposebastes+imus+Garman%2C+1899%22+OR+raw_taxon_name%3A%22Ectreposebastes+niger%22+OR+raw_taxon_name%3A%22Ectreposebastes+niger+%28Fourmanoir%2C+1971%29%22. Accessed 19 January 2017.

ALA 2020. — Atlas of Living Australia website at https://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:e6bc1770-9be1-4d4a-a876-2c6740f7fd97. Accessed 17 July 2020.

Badrudin B., Nugroho D. & Suman A. 2007. — The most abundance and the very rare species in the deep sea fish community in the Western Sumatera, Eastern Indian Ocean. *Indonesian Fisheries Research Journal* 13: 17-30.

Balanov A. A., Moku M., Kawaguchi K. & Shinohara G. 2009. — Fishes collected by commercial size midwater trawls from the Pacific Coast off Northern Japan, *in* Fujita T. (ed), Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan. *National Museum of Nature and Science Monographs* 39: 655-681.

Bianchi G., Lundsør E. & Hamukuaya H. 2004. — On Namibia's marine fish diversity, *in* Sumaila U. R., Boyer D., Skogen M. D. & Steinshamn S. I. (eds), *Namibia's Fisheries: Ecological, economic and social aspects*. Eburon Academic Publishers, Delft: 75-98.

Campana S. E. 2004. — Photographic atlas of fish otoliths of the Northwest Atlantic Ocean. *Canadian Special Publication of Fisheries and Aquatic Sciences*. NRC Research Press, Ottawa, 284 p.

Campana S. E. 2005. — Otolith science entering the 21st century. *Marine and Freshwater Research* 56: 485-495.

Cherel Y., Romanov E. V., Annasawmy P., Thibault D. & Ménard F. 2020. — Micronektonic fish species over three seamounts in the southwestern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* 176: 104777. https://doi.org/10.1016/j.dsr2.2020.104777

Choy C. A., Portner E., Iwane M. & Drazen J. C. 2013. — Diets of five important predatory mesopelagic fishes of the central North Pacific. *Marine Ecology Progress Series* 492: 169-184. https://doi.org/10.3354/meps10518

Chung M.-T. 2015. — Functional and life-history traits in deep-sea fishes. Ph. D. Thesis. University of Southampton, Southampton, 175 p.

Collette B. B. & Uyeno T. 1972. — *Pontinus niger*, a synonym of the Scorpionfish, *Ectreposebastes imus*, with extension of its range to Japan. *Japanese Journal of Ichthyology* 19: 26-28. https://doi.org/10.11369/JJI1950.19.26

De Paiva C. C., De Araújo M. E., Caires R. A., Salles R., De Medeiros R. S. & Da Cruz Lotufo T. M. 2011. — Six new records of deep-sea fish off north-eastern Brazil. *Marine Biodiversity Records* 4 E9. https://doi.org/10.1017/S1755267210001247.

Eduardo L. N., Mincarone M. M., Villarins B. T., Frédou T., Lira A. S., Bertrand A. & Lucena-Frédou F. 2019. — Length-weight relationships of eleven mesopelagic fishes from oceanic islands of the Southwestern Tropical Atlantic. *Journal of Applied Ichthyology* 35: 605-607. https://doi.org/10.1111/jai.13840

Eschmeyer W. N. 1969. — A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). *Occasional Papers of the California Academy of Sciences* 79: 1-143.

Eschmeyer W. N. 1986. — Scorpaenidae, *in* Smith M. M. & Heemstra P. C. (eds), *Smith's Sea Fishes*. Springer-Verlag, London-Paris-Tokyo: 463-478

Eschmeyer W. N. & Collette B. B. 1966. — The scorpionfish subfamily Setarchinae, including the genus *Ectreposebastes*. *Bulletin of Marine Science* 16: 349-375.

Eschmeyer W. N. & Randall J. E. 1975. — The scorpaenid fishes of the Hawaiian Islands, including new species and new records (Pisces: Scorpaenidae). *Proceedings of the California Academy of Sciences*, 45th ser., 40: 265-334.

Eschmeyer W. N. & Fricke R. (eds) 2012. — Catalog of fishes electronic version (12.02.2012). http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Escánez A. & Brito A. 2011. — First record of the midwater scorpionfish *Ectreposebastes imus* (Scorpaeniformes: Setarchidae) in the subtropical eastern Atlantic (Canary Islands). *Marine Biodiversity Records* 4(e78): 1-3. http://doi.org/10.1017/S1755267211000704

Fourmanoir P. 1971. — Notes ichtyologiques (II). *Cahiers ORSTOM, Série Océanographie* 8 (3) (1970): 35-46.

Fourmanoir P. 1976. — Formes post-larvaires et juvéniles de poissons côtiers pris au chalut pélagique dans le sud-ouest Pacifique. *Cahiers de l'Indo-Pacifique* 19: 47-88.

Frable B. W., Wagman D. W., Frierson T. N., Aguilar A. & Sidlauskas B. L. 2015. — A new species of *Sebastes* (Scorpaeniformes: Sebastidae) from the northeastern Pacific, with a redescription of the blue rockfish, *S. mystinus* (Jordan and Gilbert, 1881). *Fishery Bulletin* 113: 355-377. http://doi.org/10.7755/FB.113.4.1

Fricke R. 1999. — Fishes of the Mascarene Islands (Réunion, Mauritius, Rodriguez). An annotated checklist, with descriptions of new species, *Theses Zoologicae* Volume 31. Koeltz Scientific Books, Königstein, 759 p.

Fricke R., Mulochau T., Durville P., Chabanet P., Tessier E. & Letourneur Y. 2009. — Annotated checklist of the fish species (Pisces) of La Réunion, including a Red List of threatened and declining species. *Stuttgarter Beiträge Zur Naturkunde A*, Neue Serie 2: 1-168.

Fricke R., Eschmeyer W. N. & Van der Laan R. (eds) 2020. — Eschmeyer's catalog of fishes: genera, species, references. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 20 July 2020.

Froese R. & Pauly D. (eds) 2019. — FishBase. World Wide Web electronic publication. www.fishbase.org, version (12/2019).

GBIF.org 2017. — GBIF Occurrence Download http://doi.org/10.15468/dl.nni1tq. Accessed 19 January 2017.

GBIF.org 2020. — GBIF Occurrence Download https://doi.org/10.15468/dl.5uezy2. Accessed 22 July 2020.

GEBCO 2003. IOC, IHO and BODC. — Centenary Edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool.

GEBCO 2016. — The GEBCO_2014 Grid, version 20150318. www.gebco.net

González J. A., Martins A., Santana J. I., Triay-Portella R., Monteiro C., Garcia-Martin V., Jiménez S., González-Lorenzo G., Pajuelo J. G., Lorenzo J. M. & Biscoito M. 2014. — New and rare records of teleost fishes from the Cape Verde Islands (eastern-central Atlantic Ocean). *Cybium* 38: 289-300.

Govindam S. V. S., Sreedhar U. & Kumari B. M. 2013. — Abundance, bathymetric distribution and diversity of deep sea demersal finfish resources along the south-west coast of India. *Indian Journal of Fisheries* 60: 1-6.

Granadeiro J. P. & Silva M. A. 2000. — The use of otoliths and vertebrae in the identification and size-estimation of fish in predator-prey studies. *Cybium*, 24: 383-393.

Grove J. S. & Lavenberg R. J. 1997. — The fishes of Galápagos Islands. Stanford University Press, Stanford, 912 p.

Hashim M. 2012. — Distribution, diversity and biology of deep-sea fishes in the Indian EEZ. Ph.D. Thesis. Cochin University of Science and Technology, Kochi, India, 184 p.

Hulley P. A. & Lutjeharms J. R. E. 1989. — Lanternfishes of the southern Benguela region. Part 3. The pseudoceanic-oceanic interface. *Annals of the South African Museum* 98: 409–435.

IHO (International Hydrographic Organization) 1953. — Limits of oceans and seas. 3rd edition. International Hydrographic Organization, Monaco, Special Publication (S-23) 23: 38 p.

Ivanova N. V., Zemlak T. S., Hanner R. H. & Hebert P. D. N. 2007. — Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Resources* 7: 544-548.

Jobling M. & Breiby A. 1986. — The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia* 71: 265-274.

Kai Y. & Nakabo T. 2013. — Taxonomic review of the *Sebastes pachycephalus* complex (Scorpaeniformes: Scorpaenidae). *Zootaxa* 3637: 541-560.

Kawai T., Tashiro F., Imamura H. & Aungtonya C. 2017. — Deep-sea fishes collected from the Andaman Sea by R/V Chakratong Tongyai during 1996–2000. Part 1: Order Scorpaeniformes. *Phuket Marine Biological Center Research Bulletin* 74: 23-32.

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. — MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35:1547-1549.

Letourneur Y., Chabanet P., Durville P., Taquet M., Teissier E., Parmentier M., Quéro J.-C. & Pothin K. 2004. — An updated checklist of the marine fish fauna of Reunion Island, south-western Indian Ocean. *Cybium* 28:199-216.

Lohmeyer U. 1996. — Narrative and major results of the Indonesian-German Module (II) of the JETINDOFISH Project, August 1979 to July 1981, *in* Pauly D. & Martosubroto P. (eds), Baseline Studies of Biodiversity: The Fish Resources of Western Indonesia. *ICLARM Studies and Reviews* 23: 77-90.

Lombarte A., Chic Ò., Parisi-Baradad V., Olivella R., Piera J. & García-Ladona E. 2006. — A web-based environment for shape analysis of fish otoliths. The AFORO database. *Scientia Marina* 70: 147-152.

Mandrytsa S. A. 1990. — On the validity of *Ectreposebastes niger* and distribution of species of the genus Ectreposebastes (Pisces, Scorpaenidae), *in* Trudy Zoologicheskogo Instituta, Akademii Nauk SSSR 213: 29-34. [In Russian, English summary.]

Marsac F., Annasawmy P., Noyon M., Demarcq H., Soria M., Rabearisoa N., Bach P., Cherel Y., Grelet J. & Romanov E. 2020. — Seamount effect on circulation and distribution of ocean taxa in the vicinity of La Pérouse, a shallow seamount in the southwestern Indian Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 176: 104715. https://doi.org/10.1016/j.dsr2.2020.104806

Maruyama K. & Ono K. 1975. — On the specimens of Scorpaenid fish *Ectreposebastes imus* from off Kamaishi, Japan. *Japanese Journal of Ichthyology* 21: 233-234.

Moser H. G., Ahlstrom E. H. & Sandknop E. M. 1977. — Guide to the Identification of Scorpionfish Larvae (Family Scorpaenidae) in the Eastern Pacific With Comparative Notes on Species of Sebastes and Helicolenus From Other Oceans. *NOAA Technical Report NMFS* 402. NOAA NMFS. 71 p.

Motomura H. & Struthers C. D. 2015. — The Fishes of New Zealand. Volume Three. Systematic Accounts. 154 Family Setarchidae (1083-1085), *in* Roberts C. D., Stewart A. L. & Struthers C. D. (eds), *The Fishes of New Zealand. Volume 3.* Te Papa Press, Wellington: 577-1152.

Natural History Museum 2014. — Dataset: Collection specimens. Resource: Specimens. Natural History Museum Data Portal (data.nhm.ac.uk). https://doi.org/10.5519/0002965, Retrieved: 13:11 26 December 2018 (GMT).

OBIS 2020. — Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. https://obis.org/

Paulin C. D. 1982. — Scorpionfishes of New Zealand (Pisces: Scorpaenidae). *New Zealand Journal of Zoology* 9: 437-450. http://doi.org/10.1080/03014223.1982.10423875

Pauly D., Cabanban A. & Torres F. S. B. 1996. — Fishery Biology of 40 trawl-caught teleosts of Western Indonesia, *in* Pauly D. & Martosubroto P. (eds), Baseline Studies of Biodiversity: The Fish Resources of Western Indonesia. *ICLARM Studies and Reviews* 23: 135-216.

Poss S. G. & Eschmeyer W. N. 2002. — Scorpaenidae, *in* Carpenter K. E. (ed) *The living marine resources of the Western Central Atlantic. Volume 2: Bony fishes part 1 (Acipenseridae to Grammatidae).* FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. Rome, FAO: 1232-1265.

Puillandre N., Lambert A., Brouillet S. & Achaz G. 2012. — ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* 21:1864-1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Ratnasingham S. & Hebert P. D. N. 2007. — BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* 7: 355-364. https://doi.org/10.1111/j.1471-8286.2006.01678.x

Reid S. B., Hirota J., Young R. E. & Hallacher L. E. 1991. — Mesopelagic-boundary community in Hawaii: Micronekton at

the interface between neritic and oceanic ecosystems. *Marine Biology* 109: 427-440. https://doi.org/10.1007/BF01313508
Robertson D. R. & Van Tassell J. 2019. — Shorefishes of the Greater Caribbean: online information system. Version 2.0 Smithsonian Tropical Research Institute, Balboa, Panamá. https://biogeodb.stri.si.edu/caribbean/en/pages. Accessed 5 August 2020.
Romanov E. V. & Zamorov V. V. 2002. — First record of a yellowfin tuna (*Thunnus albacares*) from the stomach of a longnose lancetfish (*Alepisaurus ferox*). *Fishery Bulletin* 100: 386–389.
Romanov E. V., Bach P., Rebik S. T., Le Turc A. & Séret B. 2013. — First pelagic record of the velvet dogfish *Zameus squamulosus* (Günther, 1877) (Squaliformes) from the southwestern Indian Ocean and some notes on its regional distribution. *Zoosystema* 35: 11-23. https://doi.org/10.5252/z2013n1a2
Sabaj M. H. 2019. — Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An Online Reference. Version 7.1 (21 March 2019). American Society of Ichthyologists and Herpetologists, Washington, DC. Electronically accessible at: https://asih.org/standard-symbolic-codes/about-symbolic-codes
Saitou N. & Nei M. 1987. — The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4: 406-425.
Scherbachev Y. N., Levitsky V. N. & Portsev P. I. 1978. — On records of the rare species of deep-sea fishes from off Southern Africa. *Trudy Instituta Okeanologii* 11: 185-194. [In Russian].
Smale M. J., Watson G. & Hecht T. 1995. — Otolith atlas of southern African marine fishes. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology*. Issue 1. Grahamstown, xiv, 253 p., 149 plates.
Strømme T., Alvheim O. & Groeneveld J. 2010. — Cruise report “Dr. Fridtjof Nansen” Mauritius and Southern Mascarene: Pelagic Ecosystem Survey, SWIOFP/ FAO 2010, Cruise 1 6-21 December 2010. Preliminary report. Institute of Marine Research, Bergen.
Tamura K., Nei M. & Kumar S. 2004. — Prospects for inferring very large phylogenies by using the neighbor-joining method. *Proceedings of the National Academy of Sciences* 101: 11030-11035.
Tatsuta N., Imamura H., Nakaya K., Kawai T., Abe T., Sakaoka K., Takagi S. & Yabe M. 2014. — Taxonomy of mesopelagic fishes collected around the Ogasawara Islands by the T/S Oshoro-Maru. *Memoirs of the Graduate School of Fisheries Sciences Hokkaido University* 56: 1-65.
Tuset V. M., Lombarte A. & Assis C. A. 2008. — Otolith atlas for the western Mediterranean, north and central eastern Atlantic. *Scientia Marina* 72S1: 7-198.
Venu S. 2013. — Deep-sea fish distribution along the south-west region of Indian EEZ, *in* Venkataraman K., Sivaperuman C. & Raghunathan C. (eds), *Ecology and Conservation of Tropical Marine Faunal Communities*. New York, Dordrecht, London: Springer-Verlag Berlin Heidelberg: 261-281. https://doi.org/10.1007/978-3-642-38200-0
WoRMS Editorial Board 2018. — World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 1 December 2018. https://doi.org/10.14284/170

Submitted on 28 January 2020;
accepted on 9 September 2020;
published on 1 June 2021.