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Encountering the morphological and molecular complexity in the bramble shark *Echinorhinus* cf. *E. brucus* (Bonnaterre 1788) from the Oman Sea

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Abstract

This is the first simultaneous morphological and barcoding characterization with the cytochrome c oxidase subunit I (COI) of the bramble shark *Echinorhinus* from the coast of Oman. The morphology of the specimen was consistent with previous records of *Echinorhinus* from the Gulf of Oman and the Arabian Sea (Northwestern Indian Ocean). However, the new COI haplotype clustered together with homologous sequences of specimens from India. The specimen from Oman distinguished morphologically and genetically from an *E. brucus* from the Western Atlantic Ocean on the shape and size of the dermal denticles, the proportions of twelve morphometric measurements (differences $\geq 3\%$) and the genetic p-distance = 3.8% of the COI fragment. The haplotype reported here increases the genetic diversity in genus *Echinorhinus* in the Northwest Indian Ocean, demonstrates conspecificity between specimens from Oman and *Echinorhinus* cf. *E. brucus* distributed in India and extends its range of distribution. The limited morphological and molecular data available constrained assigning our specimen to other than *Echinorhinus* cf. *E. brucus* (Bonnaterre, 1788). Our findings highlight the urgent need of morphological review, redescription and the assignment of a neotype in order to guarantee accurate species identification and thus effective conservation measures for these deep-sea sharks. The existence of a third living species in the genus is briefly discussed.

Introduction

Currently, the genus *Echinorhinus* includes two living species: the bramble shark *Echinorhinus brucus* (Bonnaterre, 1788) and the prickly shark *E. cookei* Pietschmann, 1928 (Bernardi and Powers, 1992; Compagno *et al.*, 2005; Ebert *et al.*, 2021; Fricke *et al.*, 2022). The genus shows circumglobal distribution from cold-temperate to tropical seas occurring in continental and insular shelves and slopes near the bottom from 4 to 1214 m (Nelson *et al.*, 2016; Ebert *et al.*, 2021). The scant sighting and catching records show that both species co-occur in Australia, New Zealand and Japan (Taniuchi and Yanagisawa, 1983). However, *E. cookei* has been mostly reported along the eastern Pacific and Hawaii (Crow *et al.*, 1996; Long *et al.*, 2011; Calle-Morán and Béarez, 2020), whereas *E. brucus* is majorly reported in the Western (North Carolina and Gulf of Mexico), Caribbean Sea (Venezuela), South America (Brazil, Argentina, Colombia), and Eastern Atlantic (Europe, Africa), Mediterranean, both coasts of India and Oman (Barcellos and Pinedo, 1980; Schwartz, 1993; Caille and Olsen, 2000; Javadzadeh *et al.*, 2011; Fariña *et al.*, 2014; Anguila *et al.*, 2016; Ray and Mohapatra, 2020; Ebert *et al.*, 2021). The occurrence of a new species in the genus *Echinorhinus* aside from *E. brucus* distributed in the western Indian Ocean has been hypothesized based on the genetic distances of the NADH dehydrogenase subunit 2 (NADH2) (Henderson *et al.*, 2016). This work deals with a new geographic record, morphological and mitochondrial characterization of the bramble shark *Echinorhinus* cf. *E. brucus* in the Oman Sea.

Material and methods

One specimen of the bramble shark *Echinorhinus* cf. *E. brucus* was incidentally caught during the shark fishing season in January 2021 at Bandar Al Khairan, Muscat, Oman. The specimen was caught with a long line approximately at 80 m depth. The fisherman donated the dead shark to the authors (after arrival from the landing site to the fish market). Then, the shark was transported in a cool box to the facilities at the Fishery Quality Control Center (FQCC) in Muscat, Oman. The taxonomic identity to genus level of the specimen was corroborated following Compagno and Niem (1998). Then, 52 morphometric and meristic characters



were recorded (in centimeters, cm) and compared with previous published data (Fariña *et al.*, 2014) (Table 1).

Muscle tissue of the shark was biopsied and used for further DNA barcoding characterization. The genomic DNA was extracted with the phenol-chloroform isoamyl technique (Green and Sambrook, 2012). A fragment of cytochrome oxidase I (COI) was amplified through polymerase chain reaction (PCR) using the primer set FishF1 5'-TCA ACC AAC CAC AAA GAC ATT GGC AC-3' and FishR1 5'-TAG ACT TCT GGG TGG CCA AAG AAT CA-3' (Ward *et al.*, 2005). Each PCR reaction was performed with the PuReTaq Ready-To-Go (RTG) PCR Beads (GE Healthcare) in a 25 µl total final volume consisting of 22 µl of ultrapure water, 0.5 µl (10 µM) of each primer and 2 µl of gDNA template. Cycling conditions consisted of an initial step of 15 min at 95°C followed by 35 cycles of denaturation 60 s at 94°C, annealing 60 s at 60°C, and extension 120 s at 72°C followed by a final extension of 10 min at 72°C. The PCR assay was carried out using a thermal cycler Prolex PCR system (Applied Biosystem). Both gDNA and PCR products were visualized in 1% agarose gel stained with ethidium bromide and documented with a Chemi XRS Gel Documentation System (Nu Genius). Both strands of the PCR products were sequenced. The ExPASy translate tool (proteomic server) (<http://web.expasy.org/translate/>) was run using nucleotide sequences COI gene fragment to get amino acid sequences and open reading frame (ORF). Both nucleotide and amino acid sequences were further subjected to NCBI-BLASTX tool (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>) for matching sequences and identity of the specimen. Then, the partial sequence of COI gene obtained (642 bp) was submitted to the NCBI database under Accession No. OP476452. The evolutionary relationship of the taxa was inferred using the neighbor-joining method and the optimal tree with the sum of branch length = 0.31842936 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) and only values $\geq 70\%$ are shown in the branches. The evolutionary distances were computed using the Tamura-Nei method and are in the units of the number of base substitutions per site. The variation rate among sites was modeled with a gamma distribution (shape parameter = 1). The analysis involved 11 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 606 positions in the final dataset. Evolutionary analyses were conducted in Molecular Evolutionary Genetics Analysis version 11 (MEGA-11 software) (Tamura *et al.*, 2021). The p-distance values were compared between species.

Results

Description

The young male specimen showed cylindrical body, dorsal body surface dark purplish-gray to brown, ventral surface slightly paler; sides with scanty black spots disperse. Head moderately flattened; five pairs of gill slits. Lateral line running along upper half of body originating above the fourth gill opening and posteriorly passing through upper third of caudal peduncle curves upwards and runs to tip of upper caudal lobe. Snout short (length as mouth width, body proportion = 11%) and blunt, stout body, spiracles small (Figure 1A–C). Labial furrows very short, teeth wider than high (ratio = 1:0.44), multicuspid (20 in the upper jaw), on both jaws alike with a central oblique bladelike cusp with up to two very small cusplets on its side (Figure 1D). Darker fin margins, two small spineless dorsal fins. The second dorsal a little smaller than first one (ratio = 0.93:1), close together, the interspace between the first and second dorsal varying from about as long as base of first dorsal (Table 1). Allocated at

posterior part of the body and originate behind pelvic fin origin. The posterior base of the first dorsal fin nearly aligned with the posterior base of the pelvic fin. The anterior base of the second dorsal fin overlaps with the end tips of the pelvic fin (and the claspers slightly overpass it) (Figure 1A and B). Pectoral fins short and angular. Anal fin and subterminal notch on caudal fin absent. Denticles sparse on the whole body surface (in dorsal and ventral side), yet irregularly distributed (Figure 1A–E), thorn-like shape (cusps) with smooth basal margins rather fine ridging radiate (not stellate). The cusps are angulated, centered or slightly displaced from the basal margin. Some bases (2–3) fused into compound plates giving a circular oval shape; size varied up to 12 mm in basal diameter (Figure 1E).

Morphometry

The morphometric data of the *Echinorhinus* specimen from Bandar (this work) and Salalah, Oman showed to be distinct to the specimen *E. brucus* from Venezuela. Comparison of the morphometric characters (in proportions) showed differences ranging from 0.1 to 9.1% between the specimens of Bandar and Venezuela (Table 1, Figure 2). The proportion values of 12 morphometric characters showed conspicuous differences $\geq 3\%$. The more remarkable were the pre-caudal length, head length, pre-pelvic length, orbital-third gill slit space and pelvic posterior margin length showed the highest average proportion difference (Figure 2).

Molecular identification

The COI gene sequence of *Echinorhinus* cf. *E. brucus* from Oman represents a new haplotype and it is the third genetic identity known for the NW Indian Ocean. The phylogenetic relationships within the genus *Echinorhinus* showed three main clades. The *Echinorhinus* specimen from Oman was placed in a well-supported clade (bootstrap = 100) together with homologous sequences of the morphologically undescribed specimens from India. This group is sister to the specimen *E. brucus* from Venezuela, which formed its own clade though their relatedness was weakly supported (Bootstrap <70). The species *E. cookei* form an own well-resolved separated clade, and it is shown as the more distant relative (Figure 3).

Genetic distance

The genetic distance values (p-distance) at intraspecies level ranged between 0 and 0.05. *Echinorhinus* cf. *E. brucus* (i.e., Oman and India) showed very low average p-distance value = 0.004. A similar result was observed among *E. cookei* (average p-distance value = 0.005). Remarkably, the average genetic distance raised up to 0.017 when the specimen from Venezuela was included within the *Echinorhinus* cf. *E. brucus* group, which includes specimens from Oman and India (Table 2). Likewise, the p-distance values at interspecies level between *E. cookei*, *Echinorhinus* cf. *E. brucus* (Oman and India) and the specimen from Venezuela were very high ranging from 0.041 to 0.043, respectively (Table 2).

The pairwise nucleotide differences at intraspecies level ranged from 0 to 5, whereas at the interspecies level, the range was remarkably high 22–27 pairwise differences. Particularly, the pairwise differences of the specimen from Venezuela varied from 22 to 23 nucleotides regarding *E. cookei* and *Echinorhinus* cf. *E. brucus* (Table 2).

Discussion

The identity of the species in the genus *Echinorhinus* is controversial and has been under debate.

Table 1. Morphometry (cm) and its proportions (%) of *Echinorhinus* from Venezuela and Oman

	Character	Fariña <i>et al.</i> (2014)		Al Shajibi <i>et al.</i> (2014)		This work Bandar Al Khairan, Oman		Proportion differences
		Venezuela Adult female	%	Salalah, Oman. Adult female	%	Young male	%	Oman vs Venezuela
1	Total length	252		193		147		
2	Pre-caudal length	182.7	72.5	162	84	120	81.6	9.1
3	Head length	86.9	34.5	49	25	42	28.6	5.9
4	Pre-branchial length	44.5	17.7	39	20	31.8	21.6	4.0
5	Pre-orbital length	18.1	7.2	16.5	8.5	13	8.8	1.7
6	Eye length	4.3	1.7	4	2.1	4	2.7	1.0
7	Mouth width	30	11.9	24	12	16	10.9	1.0
8	Pre-first dorsal length	152.2	60.4	127	66	94.5	64.3	3.9
9	Pre-second dorsal length	179.7	71.3	143	74	107.5	73.1	1.8
10	First dorsal fin base	15	6.0	12	6.2	9	6.1	0.2
11	Second dorsal fin base	12.4	4.9	11	5.7	7	4.8	0.2
12	Pre-pectoral length	66.8	26.5	54	28	41	27.9	1.4
13	Pectoral fin length			22	11	15.5	10.5	
14	Pre-pelvic length	134.6	53.4	121	63	91	61.9	8.5
15	Pelvic fin length			23	12	16	10.9	
16	Head width at first gill slit			13	6.7	9	6.1	
17	Caudal peduncle height			15	7.8	9	6.1	
18	Prenarial length	13.5	5.4			11	7.5	2.1
19	Pre-oral length	19	7.5			15	10.2	2.7
20	Trunk Height	39	15.5			21.5	14.6	0.9
21	Internarial space	12.3	4.9			10	6.8	1.9
22	Nostril width	3.9	1.5			3	2.0	0.5
23	First gill slit height	12.3	4.9			7	4.8	0.1
24	Second gill slit height	11.6	4.6			8	5.4	0.8
25	Third gill slit height	11.6	4.6			9	6.1	1.5
26	Fourth gill slit height	12.2	4.8			10	6.8	2.0
27	Fifth gill slit height	15.5	6.2			11	7.5	1.3
28	First dorsal height	11	4.4			9.6	6.5	2.2
29	First dorsal base	15	6.0			7.5	5.1	0.9
30	First dorsal inner margin	6.1	2.4			5	3.4	1.0
31	Second dorsal height	13.5	5.4			9	6.1	0.8
32	Second dorsal base	12.4	4.9			7	4.8	0.2
33	Second dorsal inner margin	6	2.4			4	2.7	0.3
34	Dorsal caudal margin	62	24.6			30	20.4	4.2
35	Lower caudal margin	27.1	10.8			15.7	10.7	0.1
36	Pectoral base	17	6.7			11.5	7.8	1.1
37	Pectoral anterior margin	24.8	9.8			15	10.2	0.4
38	Pectoral posterior margin	12.4	4.9			11	7.5	2.6
39	Pectoral inner margin	13.3	5.3			7	4.8	0.5
40	Prepectoral length	66.8	26.5			40.1	27.3	0.8
41	Interdorsal space	14.1	5.6			8.5	5.8	0.2
42	Dorsalcaudal space	6	2.4			8	5.4	3.1

(Continued)

Table 1. (Continued.)

Character	Fariña <i>et al.</i> (2014)		Al Shajibi <i>et al.</i> (2014)		This work		Proportion differences
	Venezuela		Salalah, Oman.		Bandar Al Khairan, Oman		Oman vs Venezuela
	Adult female	%	Adult female	%	Young male	%	
43	Pelvic-caudal space	19.5	7.7		16	10.9	3.1
44	Pectoralpelvic space	80.5	31.9		40	27.2	4.7
45	Prebranchial length	44.5	17.7		30	20.4	2.7
46	Orbital-first gill slit space	26.5	10.5		20	13.6	3.1
47	Orbital-third gill slit space	33	13.1		29.5	20.1	7.0
48	Upper labial furrow length	2.5	1.0		2	1.4	0.4
49	Lower labial furrow length	1.7	0.7		2.4	1.6	1.0
50	Pelvic base	31.2	12.4		14	9.5	2.9
51	Pelvic anterior margin length	23.1	9.2		13.2	9.0	0.2
52	Pelvic posterior margin length	9.4	3.7		12.5	8.5	4.8

The South African representatives of the genus, as well as the Australian-New Zealand and Hawaii received separate names as supposedly distinct from the species *E. brucus* of the North Atlantic (Bigelow and Schroeder, 1948). So far *Squalus brucus* Bonnaterre, 1788, *Squalus spinosus* Gmelin, 1789, *E. spinosus* (Gmelin, 1789), *E. obesus* Smith, 1838 and *E. mccoyi* Whitley, 1931 are considered synonyms of *E. brucus*. Also, *Echinorhinus brucus* and *E. cookei* Pietschmann, 1928, were erratically classified as synonyms (Fowler, 1941; Bigelow and Schroeder, 1948; Ramachandran *et al.*, 2014).

Nowadays, *E. brucus* and *E. cookei* can be clearly distinguished from one another because the former presents spine-like non stellate dermal denticles, single or fused in plates with multiple cusps relatively big (≥ 15 mm in diameter) spread on the body. Whereas *E. cookei* is uniformly covered with numerous small denticles (4–5 mm in diameter), stellate and not fused i.e. not forming plates with multiple cusps (Garrick, 1960; Compagno and Niem, 1998; Compagno *et al.*, 2005). Garrick (1960) showed that juveniles (44–47 cm) and adults (198 cm) of *E. cookei* exhibit denticles consistently small and stellate.

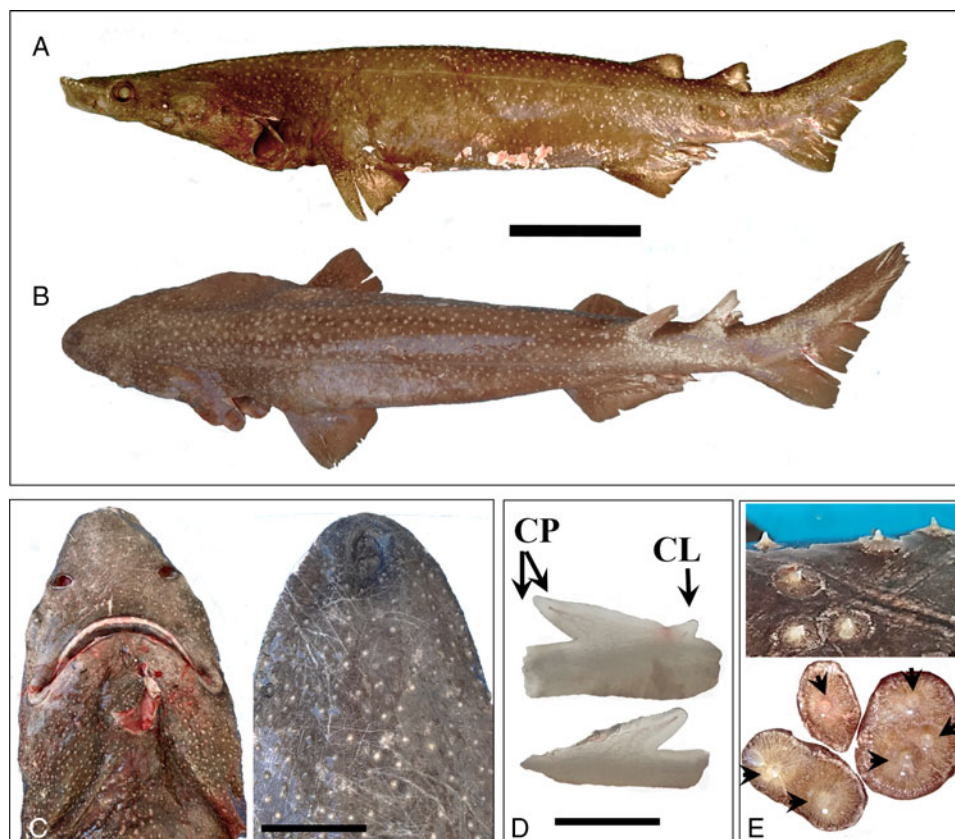


Figure 1. *Echinorhinus cf. E. brucus* (fresh specimen). A, lateral view, B, dorsal view. C-D, ventral and dorsal view of the head. D, teeth shapes. E, modified scales 1–3 general view and fused dermal denticles. Cusp (CP) (CL) (A-B: 20 cm; C: 10 cm; D: 1 cm).

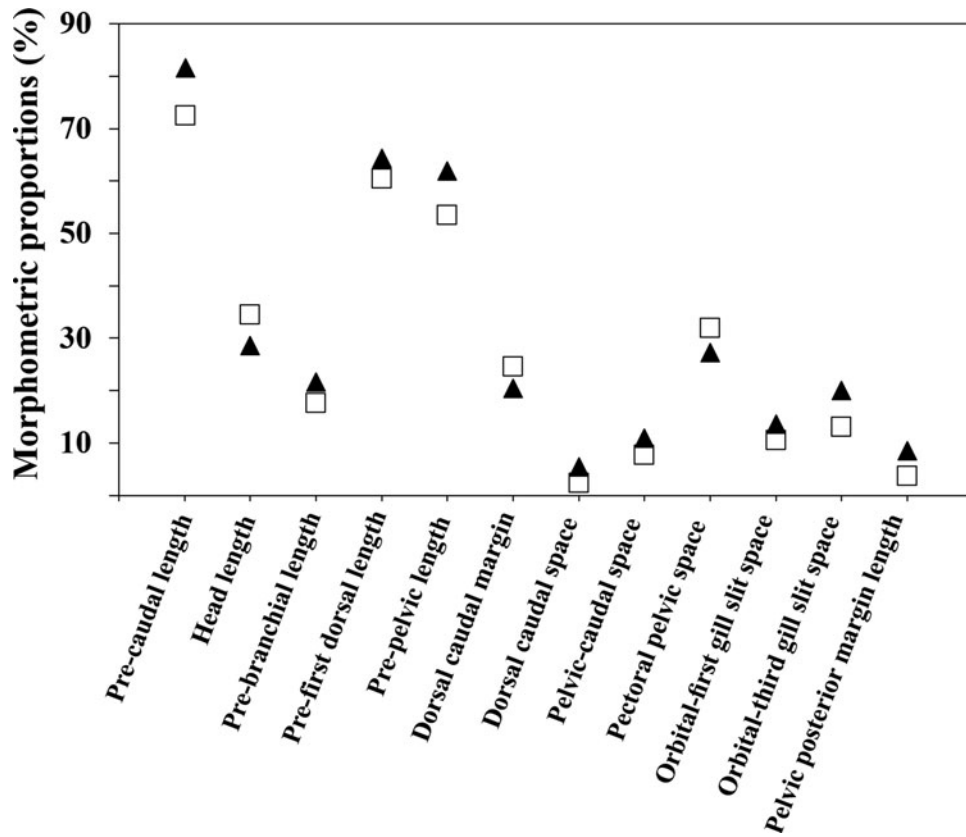


Figure 2. Morphometric comparison (proportions) between *Echinorhinus* cf. *E. brucus* from Oman (Bandar Al Khairan and off Dhalkut, Oman) (▲) and *E. brucus* from Venezuela (□).

The bramble shark, *E. brucus* is a poorly documented species known mainly from European Atlantic and Mediterranean waters. It has been reported occasionally throughout the

Atlantic but appears very rare on the western seaboard (Iglésias and Mollen, 2020). Despite that the bramble shark has scarcely been reported in Omani waters, the species has not been

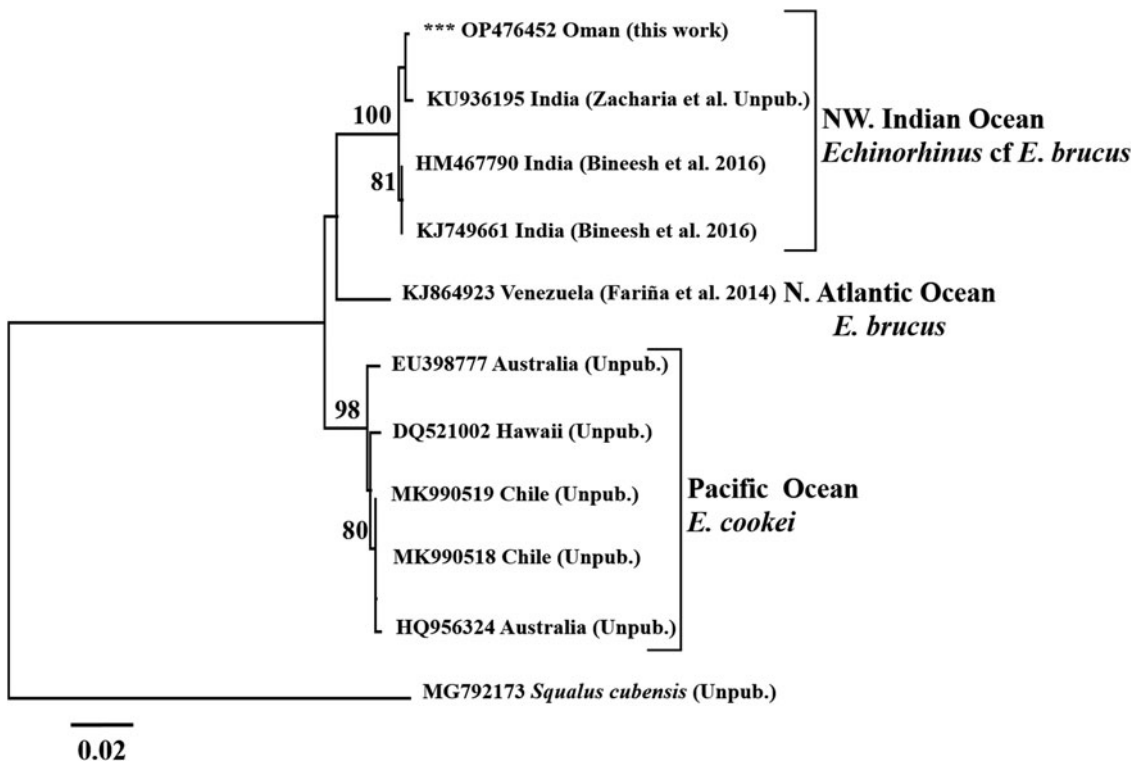


Figure 3. Neighbor-joining tree for 606 base pairs fragment of the COI gene for *Echinorhinus* cf. *E. brucus* from the present study (*) together with *E. brucus* and *E. cookei*.

Table 2. Genetic distance based on COI gene fragment (p-distance values) in the genus *Echinorhinus*

	1	2	3	4	5	6	7	8	9	10
1	<i>Echinorhinus</i> cf. <i>E. brucus</i>	OP476452 Oman	2	2	23	26	25	25	26	27
2		KU936195 India	4	4	23	26	25	25	26	27
3		HM467790 India	0	0	23	24	23	23	24	25
4		KJ749661 India	0.007	0.007	23	24	23	23	24	25
5	<i>E. brucus</i>	KJ864923 Venezuela	0.038	0.038	0.038	23	22	22	23	23
6	<i>E. cookei</i>	DQ521002 Hawaii	0.043	0.040	0.038	3	3	4	4	5
7		MK990519 Chile	0.041	0.038	0.036	0.005	0	1	1	4
8		MK990518 Chile	0.041	0.038	0.036	0.005	0.000	1	1	4
9		HQ956324 Australia	0.043	0.040	0.038	0.007	0.002	0.002	0.002	5
10		EU398777 Australia	0.045	0.041	0.038	0.008	0.007	0.007	0.008	0.008

confirmed. The first record of *E. brucus* occurred off Oman (Henderson *et al.*, 2007). Then, an adult female of *E. brucus* was recorded off Dhalkut, southern Oman, Arabian Sea (Al-Shajibi *et al.*, 2014). Henderson *et al.* (2016) made the most recent records of these sharks in Oman, which was referred to as *Echinorhinus* sp. due to a divergent sequence of the NADH2 marker regarding specimens from Australia and the western Atlantic. The phylogenetic tree based on NADH2 marker shows that *E. brucus*, *E. cookei* and the specimens from Oman and Sri Lanka are distinct species. Thus, it was hypothesized that the specimens from Oman belong to an undescribed species (Henderson *et al.*, 2016; Fernando *et al.*, 2019).

In the present work, the young adult shark from Oman exhibited single and fused denticles dispersed on the body, which formed plates with up to three multiple cusps fused (≥ 10 mm). Such characteristics, as well as the general morphology of the body, is consistent with the diagnosis of the species *E. brucus*. Thus, Oman's specimen can be distinguished from *E. cookei* based on the presence of fused denticles (which are not a feature for the latter) (Garrick, 1960). Remarkably, the specimen caught in Venezuela (reported as *E. brucus*) showed small dermal denticles (<5 mm) with intermediate morphology resembling both congeneric species i.e. fused denticles as in *E. brucus*, but stellated bases as in *E. cookei* (Fariña *et al.*, 2014). In this context, the specimen from Venezuela could not be clearly assigned morphologically to *E. brucus* or *E. cookei* (Fariña *et al.*, 2014). Comparatively, the dermal denticles of our specimen exhibit thinner and numerous trabecular fibers on their bases. However, such a characteristic is congruent with the diagnosis of *E. brucus* and consequently discriminates our specimen from both *E. cookei* and the specimen from Venezuela (referred as *E. brucus*) (Garrick, 1960; Fariña *et al.*, 2014). Likewise, male specimens of *E. brucus* occurring in India show morphological differences regarding the arrangement of denticles, the origin of lateral line and teeth (Silas *et al.*, 1969; Nair and Lal Mohan, 1971; Silas and Selvaraj, 1972). The specimen described in the present study is very similar to that one described by Nair and Lal Mohan (1971). In this regard, Iglésias and Mollen (2020) inferred that the holotype of *E. brucus*, of the collections of the Muséum national d'Histoire naturelle in Paris (MNHN's), was destroyed, lost or preserved fragmented (skin, teeth or denticles). Thus, the holotype of the species is mentioned lost in all modern references (e.g. Iglésias and Mollen, 2020; Fricke *et al.*, 2022). Currently, the MNHN's ichthyology collections only include two stuffed whole specimens of moderate size and from the Mediterranean, an embryo as well as several fragments (skins, jaws, teeth, dermal loops, skeletal parts) often without associated information and none of which is likely to be reassigned to the lost holotype (Iglésias and Mollen, 2020). Independently, morphological comparison carried out within specimens referred to as *E. brucus* in this work (i.e., specimens from Venezuela and Oman), confirms the existence of a third living species in the genus, but also exhibits the need to reassign to the lost holotype of *E. brucus*.

Regarding the genetic diversity of the genus *Echinorhinus*, very little is known partly due to the fact that most specimens recorded worldwide lack genetic characterization. Paradoxically, the scarce public data of *Echinorhinus* deposited in both the Barcode of Life Data Systems (BOLD) and GenBank lack morphological descriptions. The mitochondrial COI and NADH2 regions are relatively more used to characterize these sharks and are essential to provide new information regarding the relatedness of shark populations of the genus *Echinorhinus*. In the present work, the new COI haplotype of our specimen reveals its conspecificity with those occurring in Western India. Likewise, the overall phylogenetic relationships at both the interspecific and intraspecific levels concurred with previous findings based on the COI gene fragment

(Fariña *et al.*, 2014). Indeed, the general topology of the tree showing three main clades is congruent with previous findings based on the NADH2 region. Besides, the genetic distance values at intraspecies and interspecies levels were congruent with those obtained with the COI and NADH2 (Fariña *et al.*, 2014; Henderson *et al.*, 2016; Fernando *et al.*, 2019). Thus, the hypothesis of the occurrence of a third species in the genus *Echinorhinus* is confirmed. Nevertheless, some considerations must be taken into account: 1) the specimen identified as *E. brucus* from Venezuela (Fariña *et al.*, 2014) and North Carolina (USA) are conspecific (COI genetic identity = 99.68%, see his figure 3); 2) by integrating and comparing the morphology and genetics of the adult female from Venezuela with our specimen, it is observed that they are clearly different species, though not necessarily new; and 3) the interspecies relationships obtained with the COI and NADH2 regions need to be clarified. Specifically, in the analysis with the COI fragment *E. cookei* (i.e. specimens from Hawaii and Australia) is shown as the more distant taxon of the clade formed by *Echinorhinus* cf. *E. brucus* and *E. brucus*, whereas, with the NADH2, it is relocated as the more closely related to the 'undescribed species' (see Henderson *et al.* 2016; Fernando *et al.*, 2019).

The findings regarding the genetic analysis with COI show that the morphological characteristics used to discriminate *Echinorhinus* spp. are very limited. Further contribution is required to contrast the relevance of other morphological characters of *Echinorhinus* cf. *E. brucus* examining previous descriptions in the literature in order to clearly diagnose *Echinorhinus brucus* (*sensu stricto*) or to resurrect previous synonymized names accordingly.

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Consent for publication. Not applicable.

Conflict of interest. The authors declare that they have no conflict of interests.

Ethical standards. Not applicable.

Data. All data generated or analyzed during this study are included in this published article.

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