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Low mitochondrial genetic diversity and distribution of the goblin shark (*Mitsukurina owstoni* Jordan, 1898)

Baja diversidad genética mitocondrial y distribución del tiburón duende (*Mitsukurina owstoni* Jordan, 1898)

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ABSTRACT

Sharks (Chordata: Chondrichthyes) can live in diverse environments and have distinct lifestyles. Several species migrate and are widely distributed worldwide, particularly deep-sea sharks. The Goblin shark (*Mitsukurina owstoni*) is a deep-sea shark species characterized by its elongated snout and protrusible jaws. The goal of this study was to review the global distribution of *M. owstoni* using QGIS, based on information from scientific publications in GBIF, BOLD Systems, and GenBank. Additionally, using DNA barcoding, two newly recorded individuals collected in Madeira, Portugal, in 2022, were analyzed, and global levels of genetic diversity and population differentiation were calculated, considering all available DNA sequences of this species. This showed that the Goblin shark is distributed globally and genetic diversity between individuals is low, with only two distinct haplotypes, one of which is present globally. In summary, there is probably only one active population, with no geographic structure and high connectivity between locations, due to this species' migratory behavior.

Keywords: Deep sea, DNA barcoding, migration patterns, population structure, reproduction

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RESUMEN
Los tiburones (Chordata: Chondrichthyes) pueden vivir en diversos entornos y tener estilos de vida distintos. Varias especies migran y se encuentran ampliamente distribuidas en todo el mundo, especialmente los tiburones de aguas profundas. *Mitsukurina owstoni* es una especie de tiburón de aguas profundas, caracterizada por su hocico alargado y sus mandíbulas protráctiles. El objetivo de este estudio fue revisar la distribución global de *Mitsukurina owstoni* utilizando QGIS, con base en la información de publicaciones científicas en GBIF, BOLD Systems y GenBank. Además, mediante el código de barras de ADN, se analizaron dos nuevos individuos registrados y recolectados en Madeira, Portugal, en 2022, y se calcularon los niveles globales de diversidad genética y de diferenciación poblacional, considerando todas las secuencias de ADN disponibles para esta especie. Esto mostró que el tiburón duende se distribuye globalmente y que existe una baja diversidad genética entre los individuos, con solo dos haplotipos distintivos, uno de los cuales se encuentra presente de forma global. En conclusión, probablemente haya solo una población activa, sin estructura geográfica y con alta conectividad entre las ubicaciones, debido al comportamiento migratorio de esta especie.
Palabras clave: Mar profundo, código de barras de ADN, patrones de migración, estructura poblacional, reproducción

INTRODUCTION

Sharks, a highly diverse group within the class Chondrichthyes, are cartilaginous fish that inhabit a wide range of environments, exhibit varied lifestyles, and use different reproductive strategies. They can be found in habitats ranging from coastal and intertidal zones to the deep sea, and from tropical waters to the icy regions of the Arctic and Antarctic. As ectotherms, their body temperature is influenced by the surrounding water, making temperature a critical factor in their distribution (Ebert *et al*. 2015). These animals are capable of long distance migrations, even at smaller sizes. Their migrations can be influenced by environmental factors such as water temperature or the availability of prey (Bres, 1993). Some species also undertake vertical migrations within the water column, with daily movements being common for certain species. Tracking these patterns is challenging, as many sharks live in open and deep waters, making them difficult to observe and track in real time.

Social structures can vary by species. Some sharks form organized groups with hierarchies based on size and sex, a behaviour more commonly seen in smaller species. These groups may also be stratified by depth. In contrast, larger species tend to be solitary and more isolated (Bres, 1993; Ebert *et al*. 2015).

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Ectotherms inhabiting extremely cold waters, such as deep ocean environments, typically exhibit lower metabolic rates, slower feeding habits, and reduced growth rates compared to other species (Cotton & Grubbs, 2015; Ebert *et al*. 2015). Reproduction in deep-water Chondrichthyans is characterized by low fecundity and likely extended gestation periods. In these habitats, segregation by sex and age is common, often necessitating long migrations for mating, which incurs high energy costs (Cotton & Grubbs, 2015).

Given the homogeneity of deep-sea habitats and its lack of strict distribution boundaries, animals from these habitats tend to have a more global range. However, despite their wide distribution, their slow reproductive rates make them especially vulnerable to threats, as they cannot rapidly replace individuals lost from populations. Sharks play critical roles in food chains and are essential to the balance of ecosystems, meaning their decline can significantly impact other species.

Mitsukurina owstoni Jordan, 1898, the Goblin shark, is a large species of deep-sea shark belonging to the order Lamniformes and family Mitsukurinidae. Although this species is not currently considered endangered — its conservation status is classified by the IUCN as *Least Concern* — this assessment is based on its sporadic occurrence across a broad geographic range, where it is primarily caught as incidental bycatch in various fisheries (Finucci & Duffy, 2018). The IUCN also acknowledges limited knowledge regarding the species' biology and population size. This species occupies depths from 95 to over 1 300 meters, suggesting vertical migration in the water column (Yano *et al*. 2007; Ebert & Stehmann, 2013; Ebert *et al*. 2015). The largest recorded individual measured 617 centimeters in length, and these sharks are believed to live up to 55 years (Pollerspöck & Straube, 2020; Kukuev & Reiner, 2022). Newborns are typically around 80 to 90 centimeters long (Pollerspöck & Straube, 2020). This species is characterized by a flaccid and soft body, a flattened extended snout, and extensible jaws specialized for capturing prey in deep-sea environments. It has long, slender, cusped teeth and a whitish body with five gills (Yano *et al*. 2007; Ebert *et al*. 2015). Its diet consists of fish, invertebrates, and crustaceans (Ebert *et al*. 2015). The species is known to inhabit the Atlantic, Pacific, and Indian ocean (Yano *et al*. 2007; Ebert *et al*. 2015; Pollerspöck & Straube, 2020). Most specimens caught are small and have not reached sexual maturity, leaving the reproduction of this species and other aspects of its biology and ecology largely unknown (Yano *et al*. 2007). In Macaronesia this species is only recorded from Madeira. Cadenat & Blache (1981), recorded this species based on a female measuring 320 cm

TL (total lenght). In the Natural History Museum of Funchal there are two formalin preserved specimens, the first dated from 1956 (MMF 8196) a female with 310 cm TL, caught in 1956 by the black scabbard fish fishermen and other one dated from 2004 (MMF 36064) a male with 315 cm TL caught in a bottom long line at Funchal Bay at 2 500 m of depth in the framework of a research project (Biscoito *et al*. 2018).

In terms of conservation, it is well-known that sharks are heavily targeted for their fins and are severely affected by fishing and finning practices. These concerns highlight the urgent need to improve and expand the available information, particularly for lesser-known species (Bres, 1993; Schmidt *et al*. 2009; Cotton & Grubbs, 2015). The use of genetic information in the design of conservation strategies has gained increasing importance in recent years (Domingues *et al*. 2021). While considerable genetic data exists for many species, others — such as *M. owstoni* — remain poorly studied, with very limited information available (Larson *et al*. 2017). The goal of this study was to review *M. owstoni* global distribution, using sightings and capture records. Additionally, using DNA barcoding, we analyzed two new recorded individuals collected in Madeira, Portugal and calculated global levels of genetic diversity and population differentiation, considering all available DNA sequences of this species.

MATERIALS AND METHODS

1. Sample Collection

Two specimens of *M. owstoni* were caught off the Coast of Ilha da Madeira, Portugal, using horizontal midwater drifting longlines, in depths between 1 000 and 1 200 meters. One was caught on 18/07/22 (coordinates: 33,322; -16,4878) - Sample 1, and the other on 11/11/2022 (coordinates: 35,1947; -15,7183) - Sample 2 (Fig. 1).

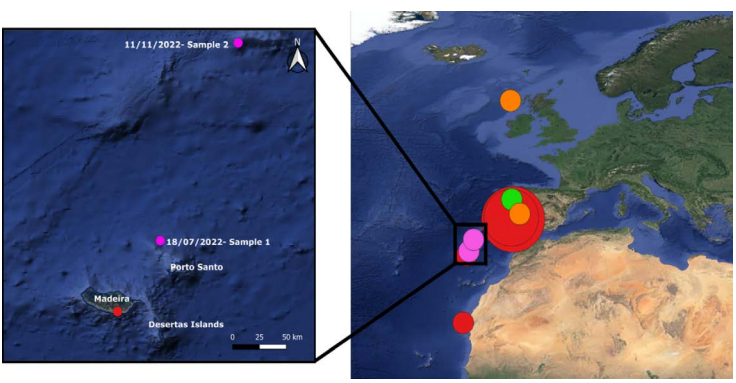

Fig. 1 Collection sites of *M. owstoni* (new records) used in this study (samples 1 & 2 in purple)
Fig. 1 Sitios de recolección de *M. owstoni* (nuevos registros) utilizados en este estudio (muestras 1 y 2 en morado)

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2. PCR and DNA sequencing

A piece of muscle from each individual was collected, conserved in 70% ethanol, and sent to ISPA- Instituto Universitário de Ciências Psicológicas e da Vida, where they were used for DNA barcoding to confirm the species identity. The methods used were based on Correia *et al*. (2021). To extract the total DNA from the muscle samples, the REDExtract-N-Amp Kit (Sigma-Aldrich) was employed, following the manufacturer instructions. After that, the same kit was used for the amplification of the cytochrome c oxidase subunit I gene, using the Fish-F1 (5'-TCAACCACCCACAAAGACATTGGCAC–3'- Ward *et al*. 2005) and Fish-R2 (5'-ACTTCA GGGTGACCGAAGAATCAGAA–3'- Ward *et al*. 2005) primers. The PCR cycling program used was 2 minutes at 95ºC, 35 cycles of 30 seconds at 94ºC, 30 seconds at 52ºC, 1 minute at 72ºC and to finalize 10 minutes still at 72ºC. Amplification success was evaluated using electrophoresis in agarose gel. The samples were sent to STABVIDA (www.stabvida.com) for sequencing. The two sequences obtained were aligned and edited in the Codon Code Aligner. The species identity was confirmed using BLAST in NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi). These sequences were also compared and aligned with the three sequences available in GenBank (EU528659; KM212006.1; KJ083251) and eight sequences available in BOLD Systems (FMVIC947-08; FMVIC948-08; FMVIC949-08, FOAE286-06, FOAG165-07; FOAL1072-10; MFSP1929-11; PHANT856-08) (Table 1). A parsimony

Table 1. Accession numbers and locations of cytochrome oxidase I sequences of *M. owstoni* used in this study
Cuadro 1. Números de acceso y ubicaciones de las secuencias de citocromo oxidasa I de *M. owstoni* utilizadas en este estudio

Sequence Accession Number	Source	Location
PP983234	This study	Madeira (33.322'' N -16.4878'' W)
PP983235	This study	Madeira (35.1947'' N -15.7183'' W)
FMVIC947-08	BOLD	Australia (38° 38' 59.9994'' S - 141° 9' 0'' E)
FMVIC948-08	BOLD	Australia (41° 15' 0'' S - 144° 4' 1.2'' E)
FMVIC949-08	BOLD	Australia (38° 0' 0'' S - 140° 0' 0''E)
FOAE286-06	BOLD	Australia (40° 31' 1.2'' S - 143° 20' 59.9994'' E)
FOAG165-07	BOLD	Taiwan (coordinates not available)
FOAL1072-10	BOLD	Australia (41° 38' 59.9994'' S - 144° 25' 1.2'' E)
EU528659	GenBank	Australia (coordinates not available)
MFSP1929-11	BOLD	Brazil (coordinates not available)
PHANT856-08	BOLD	United States of America (East Coast - coordinates not available)
KM212006.1	GenBank	Scotland (57.433'' N - 9.55'' W)
KJ083251	GenBank	Portugal (coordinates not available)

network (Fig. 2) was produced using TCS (Clements *et al*. 2002) as implemented in POPART (Leigh & Bryant, 2015).

3. Online Data search and Analysis

Sightings and capture records of *M. owstoni* were collected from scientific papers (Stewart & Clark, 1988; Duffy, 1997; Parsons *et al*. 2002; Yano *et al*. 2007; Holanda & Filho, 2008; Grijalba-Bendeck & Acevedo, 2009; Driggers *et al*. 2014; Rincon *et al*. 2014; Orlov *et al*. 2017; Iqbal *et al*. 2020; Kukuev & Reiner, 2022) and from GBIF (https://www.gbif.org/), doing an occurrence search for "*Mitsukurina owstoni*" making sure not to add duplicate records when there were different types of submissions for the same individual. The coordinates of the sequences from GenBank and BOLD were also used. With the available coordinates, using QGIS (https://qgis.org/es/site/) and Inkscape (https://inkscape.org/pt/), maps were made to show the overall known distribution of this species, as well as some possible hotspots. In the distribution map produced (Fig. 3) the points were differentiated with colors and size by the type of reference they were collected from, and by number of individuals, respectively. In a frequency of occurrence map (Fig. 4), the oceans were divided in Northeast, Northwest, Southeast and Southwest and the centroid of the observations in each area was determined. The total number of records per region was calculated and differentiated with colors.

RESULTS

1. Genetics

Genetic analyses of the cytochrome oxidase I marker revealed two new sequences, each one consisting of 647 base pairs, representing a single haplotype (GenBank accession numbers PP983234 and PP983235). The identity of this haplotype was confirmed as *M. owstoni* using BLAST, as it presents a 99.38% identity and 100% cover with a complete mitochondrial genome published for this species (GenBank accession number NC_011825.1). Upon truncating these sequences for comparison with all available sequences (Table 1), 611 bp remain, showing two different haplotypes, separated by two mutational steps (Fig. 2). Our samples correspond to this network's most common haplotype, that is shared by individuals collected from the North Atlantic and Indo-Pacific.

2. Distribution

Fig. 3 and Fig. 4 show that the goblin shark has a worldwide distribution. Clusters of observations and capture records are present in the Southwest Pacific Ocean (C), with a total of 71 points, in the Northwest Pacific (B), more specifically near Japan, with 37 points, in the Northeast Atlantic Ocean (A), particularly focused near the Iberian Peninsula, with a total of 29 points and in the Northwest Atlantic, with 25 points totals.

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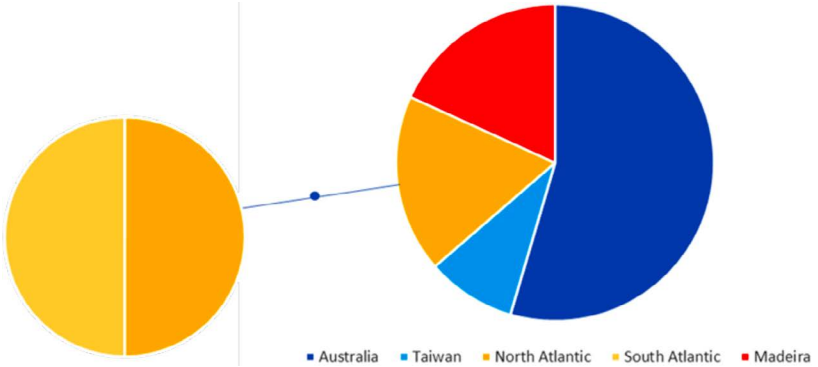

Fig. 2. Haplotype network, based on cytochrome oxidase I available sequences
Fig. 2. Red de haplotipos, basada en secuencias disponibles de citocromo oxidasa I

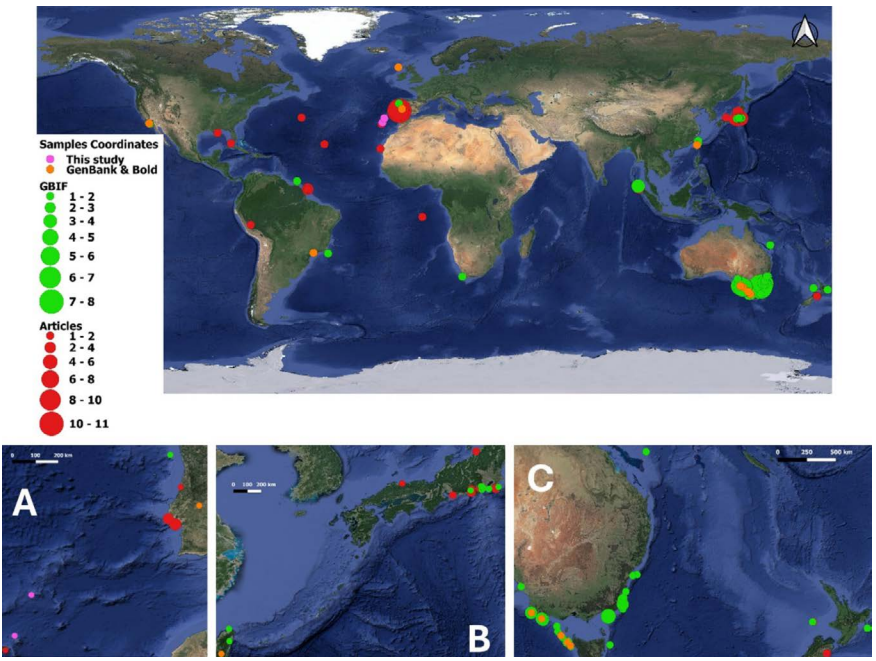

Fig. 3. *M. owstoni* distribution, hotspots zoomed in (A, B, & C), using information from GBIF, GenBank, BOLD, articles, and the samples from this study
Fig. 3. Distribución de *M. owstoni*, áreas destacadas ampliadas (A, B y C), usando información de GBIF, GenBank, BOLD, artículos y las muestras de este estudio

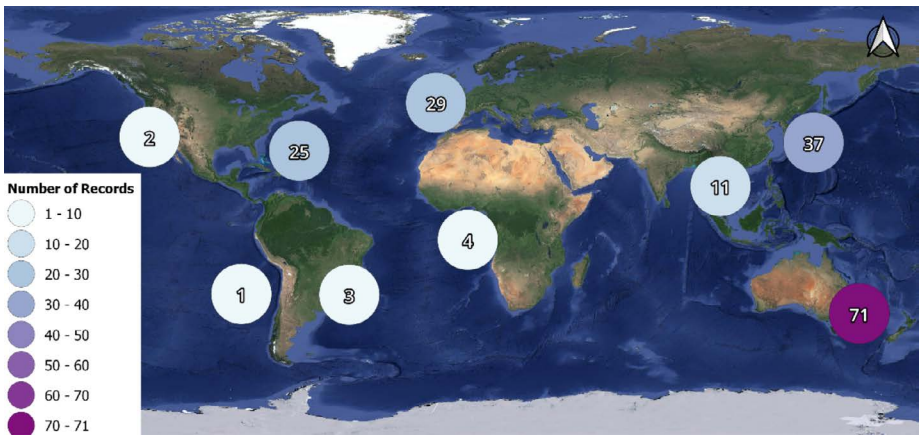

Fig. 4. Number of occurrences of *M. owstoni* by area of the different oceans, shown by centroids, using information from GBIF, GenBank, BOLD, articles, and the samples from this study

Fig. 4. Número de ocurrencias de *M. owstoni* por área de los diferentes océanos, mostradas por centroides, usando información de GBIF, GenBank, BOLD, artículos y las muestras de este estudio

There are 11 records in the Northeast Indian Ocean, 3 records in the Southwest Atlantic Ocean, 4 records in the Southeast Atlantic Ocean, 2 records in the Northeast Pacific Ocean and 1 record in the Southeast Pacific Ocean (Fig. 4).

DISCUSSION

The results of this study show that the goblin shark has a global distribution, with more capture records and sightings in the Southwest Pacific Ocean, near Australia and New Zealand, with 71 records, then in the Northwest Pacific, near Japan, with 37 records. In the Northeast Atlantic there are 29 records and, in the Northwest, Atlantic 25 records. The Northeast Indian Ocean has 11 records, in the Southeast Atlantic there were 4 records and in the Southwest Atlantic there were 3. The Northeast Pacific Ocean had 2 records and the Southeast 1 record. The genetic diversity within this species, as assessed through analysis of the COI gene, was found to be remarkably low. Only two distinct haplotypes were identified, one displaying a widespread global distribution, while the other remained restricted to the Atlantic region. These results suggest the absence of a geographic population structure.

In Smith (1986), six species of sharks from different types of habitats (three of them from deep waters) collected in New Zealand were analyzed

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to determine their levels of genetic variation. The results suggested most of the species had low heterozygosity and low genetic variation. However, not all species of sharks follow this pattern, and it is hypothesized, as suggested by Smith & Fujio (1982) for teleost fishes, that sharks specialized in a particular habitat, like angel sharks, present more diversity (as shown by Cañedo-Apolaya *et al*. 2021) than species that are habitat generalists, which have lower levels of genetic diversity, because they are disseminated over broader geographic areas and lack specific adaptations to different environments.

In Schmidt *et al*. (2009) low genetic diversity was also found between three populations of whale sharks from different geographic locations. It was suggested this was due to their regional and long-term migrations, suggesting gene flow and contact between these populations.

These findings are highly relevant to the goblin shark, a large deep-water species. As demonstrated in this study, the goblin shark has a global distribution, does not specialize in any particular habitat, and, exhibits low genetic variation among individuals from widely different locations; however, this result should be interpreted with caution due to the limited sample size of the genetic data. Additionally, as mentioned, deep-sea Chondrichthyans are segregated in the water column by size and sex, so they probably need to migrate to mate (Cotton & Grubbs, 2015). These factors and the fact that the specimens of this species probably live isolated from others, means this species most likely constitutes a single population, with no geographic structure, distributed all over the world, with high connectivity between the different places, through the migration events in the deep sea in order to mate (Bres, 1993; Yano *et al*. 2007; Cotton & Grubbs, 2015; Ebert *et al*. 2015).

This study had some limitations regarding the methods used, because some of the sources didn't provide the exact location of the catch records or observations, so the coordinates were retrieved online using the general country, city, or area, meaning they weren't as precise and sometimes would correspond to land and not to a body of water. The knowledge and study of this species is also limited because its specimens are mostly caught in areas of commercial fishing, limited to where the fishing boats operate. This means that a higher number of records in a particular area does not necessarily indicate that there are more individuals present than in other, less explored, or uncharted regions. Additionally, the number of samples of this study was very small and the number of available samples and genetic sequences for comparison is also scarce, which prevents a deep analysis of the genetic variability in this species and the possibility of making further

inferences about the population structure and its meaning.

It would be important in the future to collect more samples from different locations, sequence them and compare them with the ones already existent and present in this study, using more molecular markers, to be able to draw further conclusions about the population structure and genetics of this species.

CONCLUSION

This study showed that the goblin shark has a global distribution, and a low genetic diversity between individuals, that are likely to constitute one singular population, with no population geographic structure, with connectivity between the different locations, and that can migrate since they inhabit the deep sea.

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ATTACHMENTS

Reference	Latitude	Longitude	Number of Specimens
Yano *et al*. 2007	35.483	133.700	1
	35.133	140.250	5
	34.8499966	138.5499978	6
	37.733	138.883	3
	35.0916663	138.55166446	3
	35.1086145655	139.084109664	1
	34.6667	137.25	4
Kukuev & Reiner (2022)	38.4445100	-9.1014900	11
	40.1508	-8.85121	1
	32.6511	-16.9097	1
	38.6973	-9.42176	10
	-7.983333	0.916667	1
	-7.916667	0.950000	1
	35.466667	-51.900000	1
Grijalba-Bendeck & Acevedo (2009)	-11.35	-74.083333	1
Parsons *et al*. (2002)	28.749722	-88.570278	1
Orlov *et al*. (2017)	21.883333	-17.433333	1
Duffy (1997)	-42.483333	173.6	1
	-39.718333	178.135	1
	-42.4781973	173.52915	1
Driggers *et al*. (2014)	24.283056	-82.749722	1
Holanda & Filho (2008)	4.2525	-49.309444	1
	4.313333	-49.199722	4
	4.290556	-49.183056	2
	4.253611	-49.149722	1
	4.133056	-48.741111	1
	4.233056	-49.196389	1
	4.243611	-49.124444	4
	4.216389	-49.1275	1
	4.2	-49.175	1
	4.226667	-49.212778	2
	4.218889	-49.185833	1
	4.220556	-49.182778	1
Rincon *et al*. (2014)	23.877778	-41.883056	1
Iqbal *et al*. (2020)	4.6875	95.530556	4
Stewart & Clark (1988)	-42.500000	173.500000	1
	-39.016667	171.984444	1
	-39.001944	171.984444	1
iNaturalist contributors (2024a)	5.586655	95.319849	4
Australian Museum (2023a; 2023b; 2023c; 2023d; 2023e; 2023f)	-37.066	150.35	6
iNaturalist contributors (2024b)	-37.587268	150.387462	1
Museums Victoria (2023a)	-39.505	142.877	1

Reference	Latitude	Longitude	Number of Specimens
European Bioinformatics Institute (EMBL-EBI) & GBIF Helpdesk (2024a).	57.43	-9.55	1
Museums Victoria (2023b; 2023c; 2023d; 2023e; 2023f; 2023g; 2023h; 2023i)	-38.3853	148.719	8
European Bioinformatics Institute (EMBL-EBI) & GBIF Helpdesk (2024b)	-23.82	-40.279999	1
The International Barcode of Life Consortium (2024a).	-23.82	-40.279999	1
Shao & Lin (2014a)	24.44	121.59	1
Museums Victoria (2023j; 2023k; 2023l; 2023m; 2023n)	-38	139.95	5
The International Barcode of Life Consortium (2024b)	-38	139.95	1
European Molecular Biology Laboratory Australia (2019)	-40.52	143.35	1
Commonwealth Scientific and Industrial Research Organization (CSIRO) (2024a)	-40.75	143.51	1
Commonwealth Scientific and Industrial Research Organization (CSIRO) (2024b)	-41.73	144.46	1
European Bioinformatics Institute (EMBL-EBI) & GBIF Helpdesk (2024c)	-41.65	144.41	1
Commonwealth Scientific and Industrial Research Organization (CSIRO) (2024c)	-40.08	142.98	1
Museums Victoria (2023o; 2023p; 2023q)	-41.25	144.07	3
The International Barcode of Life Consortium (2024c)	-41.25	144.07	1
iNaturalist contributors (2024c)	-36.52	150.33	1
Australian Museum (2023g; 2023h; 2023i)	-36.52	150.33	3
Museums Victoria (2023r; 2023s; 2023t; 2023u; 2023v)	-38.77	141.3	5
The International Barcode of Life Consortium (2024d)	-38.77	141.3	1
Museums Victoria (2023w; 2023x; 2023y; 2023z; 2023aa)	-38.65	141.15	6
The International Barcode of Life Consortium (2024e)	-38.65	141.15	1
Mertz *et al*. (2024)	32.75	-118.21	1
FishBase (n. d. a.)	41.63	-9.33	1
Morris (2024a)	35.11	139.81	1
Shao & Lin (2014b)	25.3	121.56	1
Museums Victoria (2023ab)	-37.42	150.42	1
Museums Victoria (2023ac)	-36.27	150.47	1
Commonwealth Scientific and Industrial Research Organization (CSIRO) (2024d)	-41.55	148.91	1
NIWA (2014a)	-39.72	178.14	1
CSIRO National Collections and Marine Infrastructure (NCMI) Information and Data Centre (IDC) (2023a)	-35.65	150.72	1
iNaturalist contributors (2024d).	-35.65	150.72	1
NIWA (2014b)	-39.01	171.92	2
CSIRO National Collections and Marine Infrastructure (NCMI) Information and Data Centre (IDC) (2023b)	-33.78	151.98	1
iNaturalist contributors (2024e)	-33.87	151.51	1
Nakae (2024)	7.73	-53.83	1
CSIRO (1965-1978)	-20.15	153.01	1
Coetzer (2024)	-33.93	18.41	1
Morris (2024b)	35.04	139.28	1

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Reference	Latitude	Longitude	Number of Specimens
Staatliches Museum für Naturkunde Stuttgart (n. d.)	35.16	139.41	1
Chagnoux (2024)	35	138.5	2
Natural History Museum (London) (2024a)	35.27	139.28	1
FishBase (n. d. b.)	35.27	139.28	1
Morris (2024c)	35.26	139.22	1
Dillman (2018)	35.28	139.22	1
Grant *et al*. (2022)	35.23	140.45	2
Natural History Museum (London) (2024b).	35.1	139.77	1
Frable (2024)	35.1	139.77	1
South Australian Museum (2023a)	-35.1	138.83	1
South Australian Museum (2023b)	35.25	139<<<.32	1
BOLD: AAB4941 (2024)	-38.650	141.15	1
	-41.25	144.07	1
	-38	140	1
	-40.517	143.35	1
	23.553	121.021	1
	-41.65	144.417	1
	-40.52	143.35	1
	-23.5489	-46.6388	1
	32.919	-118.509	1
	57.433	-9.55	1
	39.30	-8.00	1
This study	33.322	-16.4878	1
	35.1947	-15.7183	1