

NGS data from historical museum collections help to clarify the conservation status of endangered or supposedly extinct species: the case of the Mascarene endemic freshwater shrimp *Macrobrachium hirtimanus* (Olivier, 1811)

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Abstract – *Macrobrachium hirtimanus* (Olivier, 1811) is a species of freshwater shrimp endemic to the Mascarene Islands (Réunion, Mauritius and Rodrigues). The last documented occurrences of this species date from 1980 on Réunion Island and it is thought to be now extinct. In order to determine its taxonomic distinctiveness and conservation status, historical specimens preserved in the collections of the Muséum national d'Histoire naturelle of Paris have been sequenced using a shotgun Next Generation Sequencing (NGS) method, allowing to get mitochondrial DNA barcode sequences (16S, COI) from 4 specimens collected between 1818 and 1926 on Réunion and Mauritius Islands. These sequences will be useful to build reference libraries for future eDNA surveys in the rivers of the Mascarenes that will help ascertain the conservation status of the species by guiding environmental surveys and updating the IUCN assessment. A discussion is provided on reasons leading to the possible extinction of *M. hirtimanus* as well as a list of specimens extant in museum collections worldwide.

Keywords: Conservation / mitochondrial / historical specimen / endangered species / Mascarene Islands

1 Introduction

Freshwater ecosystems are experiencing an unprecedented biodiversity crisis, with species disappearing at a rate far exceeding that of terrestrial and marine environments (Sayer *et al.*, 2025). Habitat destruction, pollution, climate change, and the introduction of invasive species are among the major drivers of this decline. Dams and water diversions disrupt hydrological connectivity, while deforestation and agricultural expansion degrade water quality (Dudgeon, 2019). Freshwater species, particularly those with restricted ranges, are highly vulnerable to these disturbances. Among the most affected are insular freshwater taxa, whose small, isolated populations are exceptionally sensitive to habitat alterations and biological invasions (Dudgeon *et al.*, 2006; Strayer and Dudgeon, 2010).

The Mascarene Archipelago, located east of Madagascar in the Indian Ocean, comprises Réunion Island (a French overseas

department) and the sovereign state of Mauritius, which includes the islands of Mauritius and Rodrigues. Like many tropical oceanic islands, the Mascarenes host a highly endemic freshwater fauna, shaped by long-term isolation and limited colonization events (Keith *et al.*, 2006). However, island species are particularly susceptible to anthropogenic pressures, and the Mascarenes have already witnessed the loss of several iconic endemic species, such as the dodo (*Raphus cucullatus* (Linnaeus, 1758)) in Mauritius and the Réunion giant tortoise (*Cylindraspis indica* (Schneider, 1783)) (Fernández-Palacios *et al.*, 2021). The next potential addition to this list of extinct species may be *Macrobrachium hirtimanus* (Olivier, 1811), a freshwater shrimp endemic to the Mascarene Islands notable for its unique morphology among regional congeners, particularly its large, spine-covered chelae.

Originally described as *Palaemon hirtimanus* by Olivier (1811) from specimens collected during the Baudin expedition, the species was later transferred to the genus *Macrobrachium* by Holthuis (1950). Its distribution was initially thought to extend to the Malay Archipelago due to confusion with *M. lepidactyloides* (De Man, 1892), but

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Holthuis (1952) later reinstated it as a distinct species restricted to the Mascarenes. Historical records indicate that *M. hirtimanus* was already rare by the late 20th century. Starmühlner (1977, 1979) failed to report it during his hydrobiological surveys, and Kiener and Duchochois (1981) collected specimens from only four rivers of Réunion Island in 1980. The species has not been recorded since these observations, while another species, *M. lepidactylus* (Hilgendorf, 1879), was first reported in the region in the 1990s (Keith and Vigneux, 2000).

The disappearance of *M. hirtimanus* aligns with the introduction or expansion of *M. lepidactylus*, an African/Malagasy species that occupies similar habitats. The two species have never been documented in synchronous sympatry, raising the question of whether *M. hirtimanus* was competitively displaced. Invasive *Macrobrachium* species have been implicated in the decline of native freshwater crustaceans elsewhere, such as *Macrobrachium lar* in Pacific islands (De Grave *et al.*, 2015). Additionally, habitat destruction and poaching have likely contributed to the decline of *M. hirtimanus*, as observed in other insular freshwater decapods (Keith *et al.*, 1999).

Determining the extinction status of *M. hirtimanus* is crucial for conservation planning. If the species persists in undetected populations, targeted conservation actions could be implemented, including habitat protection and control of invasive species. Conversely, confirming its extinction would reinforce the need for stricter biodiversity management policies in the Mascarenes, particularly regarding invasive species monitoring. Advances in environmental DNA (eDNA) analysis provide an opportunity to detect rare or cryptic species that elude conventional sampling methods, as demonstrated in recent rediscoveries of presumed-extinct amphibians (Lopes *et al.*, 2021). The generation of DNA reference sequences from museum specimens of *M. hirtimanus* could thus facilitate future eDNA surveys, improving the capacity to monitor freshwater biodiversity in the Mascarenes.

Integrative taxonomy is a powerful tool to differentiate between species when a single dataset proves to be unsatisfactory. This approach has been successful to solve taxonomical problems in freshwater shrimps (de Mazancourt *et al.*, 2018, 2019a) and especially in the genus *Macrobrachium* (Castelin *et al.*, 2017; Chow *et al.*, 2022). However, in order to use DNA to characterise the species, it is better to work with fresh (*i.e.*, recent enough) specimens that have been correctly preserved. In our case, the problem is that the most recent specimens at our disposal – those collected by Kiener in 1980 – have reportedly been fixated in formalin, which prevents sequencing. The next most recent specimens available are those reported by Roux (1934) collected in 1926 and preserved in ethanol. As DNA tends to degrade with time, it will be difficult to obtain sequences from them through regular PCR and Sanger sequencing as it is usually done for DNA barcoding.

Recent advances in sequencing methods that do not require a PCR step have become increasingly accessible, enabling the recovery of diagnostic sequences from challenging samples (Burrell *et al.*, 2015; Raxworthy *et al.*, 2021). In this study, we apply Next Generation Sequencing (NGS) technology to retrieve mitochondrial DNA sequences from historical museum specimens of *M. hirtimanus*. NGS methods, such

as the Illumina platform used here, theoretically allow for the analysis of the full mitochondrial genome (>18 kb). However, due to the fragmented state of DNA in old specimens, the results are likely incomplete, with only barcode regions of the mitogenome, such as the COI and 16S markers, being recoverable. These fragments, though limited, are sufficient for comparing the obtained sequences with barcode reference databases to confirm the identification of the samples.

We compiled a list of available *M. hirtimanus* specimens from historical museum collections and selected several from the Muséum national d'Histoire naturelle for sequencing, which was successful. The comparison of the sequences obtained from these historical specimens with those of co-occurring *Macrobrachium* species will help clarify whether *M. hirtimanus* and *M. lepidactylus* are distinct species or conspecific.

Additionally, this study provides reference sequences for future eDNA-based detection efforts, which could assist in determining the current conservation status of these species. By integrating historical collections, molecular tools, and emerging biodiversity monitoring techniques, this research highlights the importance of these approaches in assessing the conservation status of endangered freshwater taxa.

2 Materials and methods

2.1 Specimens sampling

Specimens of *M. hirtimanus* were searched in various museum collections worldwide based on published records, through public databases and requests to curators. Four large male specimens from the MNHN collection were selected, including two from Mauritius and two from La Réunion to account for the intra-specific diversity across the range of the species.

2.2 DNA extraction

Muscular tissue from pleopods of the fifth pair was sampled on four specimens of *M. hirtimanus* preserved in 70-96% ethanol in the collections of the MNHN: (1) MNHN-IU-2021-8795: Mauritius, Bambous, coll. P. Carié, Feb. 1912; (2) MNHN-IU-2021-8796: Mauritius, coll. J.-R. Quoy & J.-P. Gaimard, 1818 (probably) (Fig. 1C); (3) MNHN-IU-2021-8798 and (4) MNHN-IU-2021-8799: Réunion, Rivière des Marsouins, coll. G. Petit, 1926.

These samples were extracted with a QIAmp DNA Mini Kit, frequently used when working on dry or ethanol-preserved tissues with low DNA concentration (see for example Keith and Mennesson, 2020) and forensics. The protocol was modified to increase DNA yields from degraded tissue samples from historical specimens as followed: Step n°1 unchanged, we used step n°2a (cut up to 25 mg of tissue), step n°3 the incubation was at 50°C, step n°4 unchanged, we used step n°5b by adding 400 µl Buffer AL, step n°6 with 400 µl ethanol, steps n°7, 8, 9 and 10 unchanged (Keith and Mennesson, 2020). For the elution step, we used 50 µl Buffer AE (50% AE – 50% water) and incubated at room temperature for 5 min. Since DNA was expected to be degraded and thus fragmented, extracts were quantified using a Qubit fluorimeter (Thermo and a Fragment Analyzer with similar results for both methods). This however cannot ensure the quality of the extracts

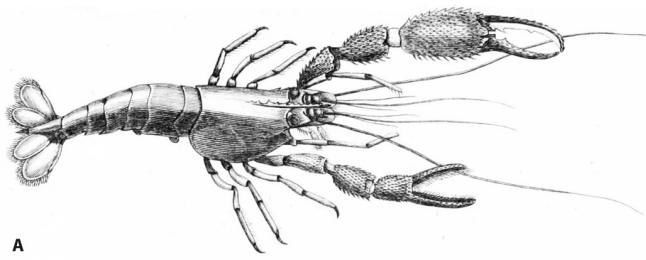


Fig. 1. *Macrobrachium hirtimanus* (Olivier, 1811). A: Drawing of the type specimen from the Paris Museum by Latreille (1818). B: The only known photograph of living specimens taken by Kiener (Kiener and Duchochois, 1981) enhanced and colored. Also the last living individuals known to have been collected. C: One of the four specimens sequenced for the present study (MNHN-IU-2021-8796).

(number/size of fragments, coverage, contamination, etc.) which can only be assessed after sequencing in our case.

2.3 Sequencing

DNA of the four specimens of *M. hirtimanus* was sequenced using shotgun-sequencing method with a NovaSeq 6000 SP Reagent Kit (300 cycles) at the the iGenSeq core facility, at the Institut du Cerveau et de la Moëlle (ICM, Paris). Shotgun libraries prepared by the third-party laboratory following their own protocol adapted to the kit and sequencer chosen were then sequenced on an Illumina® NovaSeq 6000 sequencer following manufacturer's instructions. Filtering for

quality and trimming of the reads was performed by the ICM following their own pipeline before sending us the final results.

2.4 Reads mapping

Reads were mapped against the complete mitochondrial genome of *M. bullatum* (NC_027602, Gan *et al.*, 2015) used as a reference with the "map to reference" feature implemented in Geneious Prime software (v. 2023.0.1, Biomatters Ltd.) leaving parameters as default. All NGS data was deposited in GenBank (accession number PRJNA1378948).

2.5 Phylogenetic analyses

DNA sequences of the 16S rRNA and COI gene were extracted from the consensus sequence where coverage was sufficient on the barcode regions using the consensus extraction feature implemented in Geneious Prime v. 2023.0.1. Sequences extracted were aligned using Muscle algorithm (Edgar, 2004) implemented in MEGA11 software (Tamura *et al.*, 2021) with other sequences either retrieved from GenBank (published by Aznar-Cormano *et al.*, 2015; Castelin *et al.*, 2013; 2017; Chen *et al.*, 2007; Hernawati *et al.*, 2020; Liu *et al.*, 2007 and Zimmermann, 2009) or newly produced (see de Mazancourt *et al.*, 2024 for the protocol followed). These sequences from GenBank represent the three other species of *Macrobrachium* known to occur on Réunion Island (namely *M. australe*, *M. lar* and *M. lepidactylus*) with the addition of *M. lepidactylus* that used to be synonymized with *M. hirtimanus* and *Palaemon debilis* as the outgroup. All newly produced sequences were deposited in GenBank (Tab. 2).

Neighbor-Joining phylogenetic analyses were performed on both alignments using Geneious.

3 Results

3.1 Specimens sampling

Only a handful of occurrences have been reported for *M. hirtimanus*: from Mauritius by White (1847), Milne-Edwards (1869), Sharp (1893) and Ward (1942), from Réunion Island by Roux (1934), Holthuis (1952) and Kiener and Duchochois (1981), and Rodrigues by Miers (1879). By inquiring the collections cited and some others, we could locate around 70 specimens extant in collections worldwide, collected as early as 1818 (by J.-R. Quoy & J.-P. Gaimard) and as late as 1980 (by Kiener). The lots of specimens are listed in Table 1.

3.2 DNA extraction

All four specimens included in the study contained DNA. Quantifications using a Qubit fluorimeter gave the following results: 0.858 ng/μL for specimen 1, 0.220 for specimen 2, 0.230 for specimen 3 and 0.192 for specimen 4.

3.3 Sequencing

Two sequencing runs were generated for each specimen, yielding between 48M and 59M reads per run. Reads could be mapped to the reference mitogenome of *M. bullatum* for all

Table 1. List of the specimens of *Macrobrachium hirtimanus* found in various collections worldwide.

Collection accession number	Island	Locality	Date	Collector	Number of Preservation specimens	DNA	Remarks
RMNH.CRUS.D.8817	Mauritius		entre 1867 et 1873	N. Pike	10	Ethanol	https://bioportal.naturalis.nl/multimedia/RMNH.CRUS.D.8817_0/associatedSpecimenReference =RMNH.CRUS.D.8817%40CRS&associatedSpecimenReferenceOperator=EQUALS&from=0&referer=dGVybTltYWVyb2JyYWNoaXVtk2hpcnRpbWVudXMmZmZlbnV0T00JmNpemU9MTAw
RMNH.CRUS.D.16673	Mauritius	Rivière Noire, Eaux Bonnes	13-03-1912	P. Carrié, D. d'Emmerez de Charmoy	2	Ethanol	https://bioportal.naturalis.nl/multimedia/RMNH.CRUS.D.16673_0/associatedSpecimenReference =RMNH.CRUS.D.16673%40CRS&associatedSpecimenReferenceOperator=EQUALS&from=0&referer=dGVybTltYWVyb2JyYWNoaXVtk2hpcnRpbWVudXMmZmZlbnV0T00JmNpemU9MTAw
RMNH.CRUS.D.17381	Mauritius	Cressonville	30-10-1941	R. Prader	1	Ethanol	https://bioportal.naturalis.nl/multimedia/RMNH.CRUS.D.17381_0/associatedSpecimenReference =RMNH.CRUS.D.17381%40CRS&associatedSpecimenReferenceOperator=EQUALS&from=0&referer=Z2VudXNPek1vbm9taWFsPU1hY3JvYnJhY2hpdW0mZ2VudXNPek1vbm9taWFsT3BlcmF0b3I9RVFVQUxTJmNlYmVudlbnVzPSZzdWJnZW51c09wZXJhdG9yPUVRVUFMUyZzcGVjaWZpY0VwaXRozXQ9aGlydGltYW51cyZzcGVjaWZpY0VwaXRozXRRPcGVyYXRVeW51FUFVVFUyZzcGVjaWZpY0VwaXRozXQ9JmVudmZlbnV0T00JmNpemU9MTAw
MNHN-IU-2017-11703	Reunion	Rivière Langevin		1980 A. Kiener	2	Ethanol	
MNHN-IU-2017-1442	Reunion	Rivière Langevin		1980 A. Kiener	1	Ethanol	
MNHN-IU-2017-11704	Reunion	Rivière du Mât		1980 A. Kiener	1	Ethanol	
MNHN-IU-2017-11705	Reunion	Rivière des Marsouins ?		1980 A. Kiener	1	Ethanol	
MNHN-IU-2017-1443	Reunion	Rivière de l'Est ?		1980 A. Kiener	1	Ethanol	
MNHN-IU-2017-1444	Reunion	Rivière de l'Est ?		1980 A. Kiener	1	Ethanol	
MNHN-IU-2017-11706	Reunion	Rivière de l'Est ?		1980 A. Kiener	2	Ethanol	

Table 1. (continued).

Collection accession number	Island	Locality	Date	Collector	Number of Preservation specimens	DNA	Remarks
MNHN-IU-2021-7853	Mauritius			E. Roget de Belloguet	6 Ethanol		
MNHN-IU-2021-7854	Mauritius			E. Roget de Belloguet	1 Ethanol		
MNHN-IU-2021-8795	Mauritius	Bambous	Fev 1912	P. Carié	1 Ethanol	ADN V1	cited in appendix by Roux, 1934
MNHN no number	Mauritius		1818	J.-R. Quoy & J.-P. Gaimard	2 Sec		Identified by J. W. Short le 6/12/1994
MNHN-IU-2021-8796	Mauritius		1818	J.-R. Quoy & J.-P. Gaimard	1 Ethanol	ADN V2	Edw. Det.
MNHN-IU-2021-8797	Reunion	Rivière des Marsouins	1926	G. Petit	9 Ethanol		cited by Roux, 1934
MNHN-IU-2021-8798	Reunion	Rivière des Marsouins	1926	G. Petit	1 Ethanol	ADN V3 (sp. ADN 1)	cited by Roux, 1935
MNHN-IU-2021-8799	Reunion	Rivière des Marsouins	1926	G. Petit	1 Ethanol	ADN V4 (sp. ADN 2)	cited by Roux, 1936
MNHN-Na1261	Reunion	Rivière des Marsouins	1926	G. Petit	plusieurs Ethanol		cited by Roux, 1937
MNHN-Na1259	Reunion		avant 1862	L. Maillard	6 Ethanol		
MRSNT 959	Reunion		1901	F. Sikora	2 Ethanol		cited by Holthuis, 1952
MRSNT 968	Reunion		1901	F. Sikora	2 Ethanol		cited by Holthuis, 1953
ZMB 11148	Reunion			F. Sikora	3 Ethanol		
BMNHM 1876.10	Rodrigues		1874	G. Gulliver	1 Ethanol		cited by Miers, 1879
ANSP C99	Mauritius			T. B. Wilson	2 Ethanol		cited Sharp, 1893
BMNHM 1909.2.27.7-8	Mauritius			M. Ulcoq	Sec		
QM W19980	Mauritius	Tamarin Falls			3 Ethanol		cited by Ward, 1942
BMNHM White 1 224.a-b	Indian Ocean (Mauritius?)						cited by White, 1847
BMNHM White 1 224.c-d	Indian Ocean (Mauritius?)			T. Hardwicke			cited by White, 1847

Table 2. List of the sequences included in the molecular analyses.

Species	Locality	Voucher	16S sequence	COI sequence	Reference
<i>M. hirtimanus</i>	Mauritius	MNHN-IU-2021-8795	PX667699		This study
<i>M. hirtimanus</i>	Mauritius	MNHN-IU-2021-8796	PX667700		This study
<i>M. hirtimanus</i>	Réunion	MNHN-IU-2021-8798	PX667701	PX666020	This study
<i>M. hirtimanus</i>	Réunion	MNHN-IU-2021-8799	PX667702		This study
<i>M. lepidactylus</i>	Réunion	CA3044	PX667695		This study
<i>M. lepidactylus</i>	Réunion	CA3048	PX667696		This study
<i>M. lepidactylus</i>	Réunion	CA3057	PX667697		This study
<i>M. lepidactylus</i>	Réunion	CA3062	PX667698		This study
<i>M. lepidactylus</i>	Madagascar	MC4172	PX667693		This study
<i>M. lepidactylus</i>	Madagascar	MC4175	PX667694		This study
<i>M. lepidactylus</i>	Madagascar	CA2559	PX667691		This study
<i>M. lepidactylus</i>	Madagascar	167		GU205072	Zimmermann, 2009
<i>M. lepidactylus</i>	Madagascar	168		GU205073	Zimmermann, 2009
<i>M. lepidactyloides</i>	Solomon Islands	CA2574	PX667692		This study
<i>M. lepidactyloides</i>	Papua New Guinea	CA2556	PX667690		This study
<i>M. lepidactyloides</i>	Taiwan		DQ194929		Liu <i>et al.</i> , 2007
<i>M. lepidactyloides</i>	Taiwan	MAS00009	EU493138		Chen <i>et al.</i> , 2009
<i>M. lepidactyloides</i>	Indonesia	BIC-0270		MN526230	Hernawati <i>et al.</i> , 2020
<i>M. lar</i>	Réunion	MC1361	KC506904		Castelin <i>et al.</i> , 2013
<i>M. lar</i>	Réunion	MC1378	KC506910		Castelin <i>et al.</i> , 2013
<i>M. lar</i>	Réunion	L1		GU205064	Zimmermann, 2009
<i>M. lar</i>	Réunion	L2		GU205065	Zimmermann, 2009
<i>M. lar</i>	Mayotte	L11		GU205066	Zimmermann, 2009
<i>M. lar</i>	Vanuatu	L21		GU205067	Zimmermann, 2009
<i>M. lar</i>	Samoa	L31		GU205068	Zimmermann, 2009
<i>M. australe</i>	Réunion	MC1092	KY039506		Castelin <i>et al.</i> , 2017
<i>M. australe</i>	Réunion	MC4074	KY039519		Castelin <i>et al.</i> , 2017
<i>M. australe</i>	Vanuatu	R110		GU205040	Zimmermann, 2009
<i>M. australe</i>	Mayotte	m6		GU205041	Zimmermann, 2009
<i>M. australe</i>	Samoa	P21		GU205044	Zimmermann, 2009
<i>Palaemon debilis</i>	New Caledonia	MNHN-IU-2012-1028	KP725611	KP759472	Aznar-Cormano <i>et al.</i> , 2015

four specimens of *M. hirtimanus*, with 1,415 reads for specimen 1, 695 for specimen 2, 836 for specimen 3 and 423 for specimen 4. Coverage was low overall and uneven, with similar peaks across all four specimens, the most notable one being around the 16S rRNA region (Fig. 2).

Nevertheless, coverage was sufficient to get the full length of the 16S barcode fragment (514 bp) for all four specimens and a partial COI barcode fragment (261 bp) for specimen 3 only.

3.4 Phylogenetic analysis

Phylogenetic analyses of both markers showed that *M. hirtimanus* is distinct from all the other species occurring in the Mascarenes and from *M. lepidactyloides* (Figs. 3 and 4). In 16S, all four specimens of *M. hirtimanus* clustered together in a strongly supported group (bootstrap of 99.9%) well separated from the other species (pairwise p-distances of 10.2–11.4% for 16S and 19.5% for COI to *M. lepidactyloides*, its closest relative).

4 Discussion

The sequences produced in the present study are a first step towards answering the questions raised previously.

M. hirtimanus is indeed a valid species, being clearly distinct both morphologically and genetically from the other *Macrobrachium* occurring in the area and from *M. lepidactyloides*, which used to be considered its junior synonym.

Despite numerous surveys since 1980 using traditional sampling methods (hand net and electro-fishing) on Reunion Island during which *M. hirtimanus* could not be found, it is not yet certain whether the species is extinct globally, locally, or even at all. The newly produced sequences will be useful as a reference for eDNA studies in the Mascarenes (see Zieritz *et al.*, 2022 for instance). This type of survey might detect traces of this species in the rivers of the Mascarenes, which would suggest its recent presence, as it was the case with a presumed extinct species of frog from Brazil (Lopes *et al.*, 2021) or could confirm its absence, allowing to update the status of *M. hirtimanus* for the IUCN Red List to extinct.

In any case, it is undeniable that the species has become extremely rare, if not extinct as no verified specimen has been caught since 1980, a regression seemingly concomitant with the establishment of *M. lepidactylus* in the area.

In 1991, one of us (GM) caught a specimen of *Macrobrachium* identified by L. B. Holthuis as *M. patsa* (Coutière, 1899) in the “rivière des Roches” on Réunion Island. During this prospection by electric fishing no specimen of

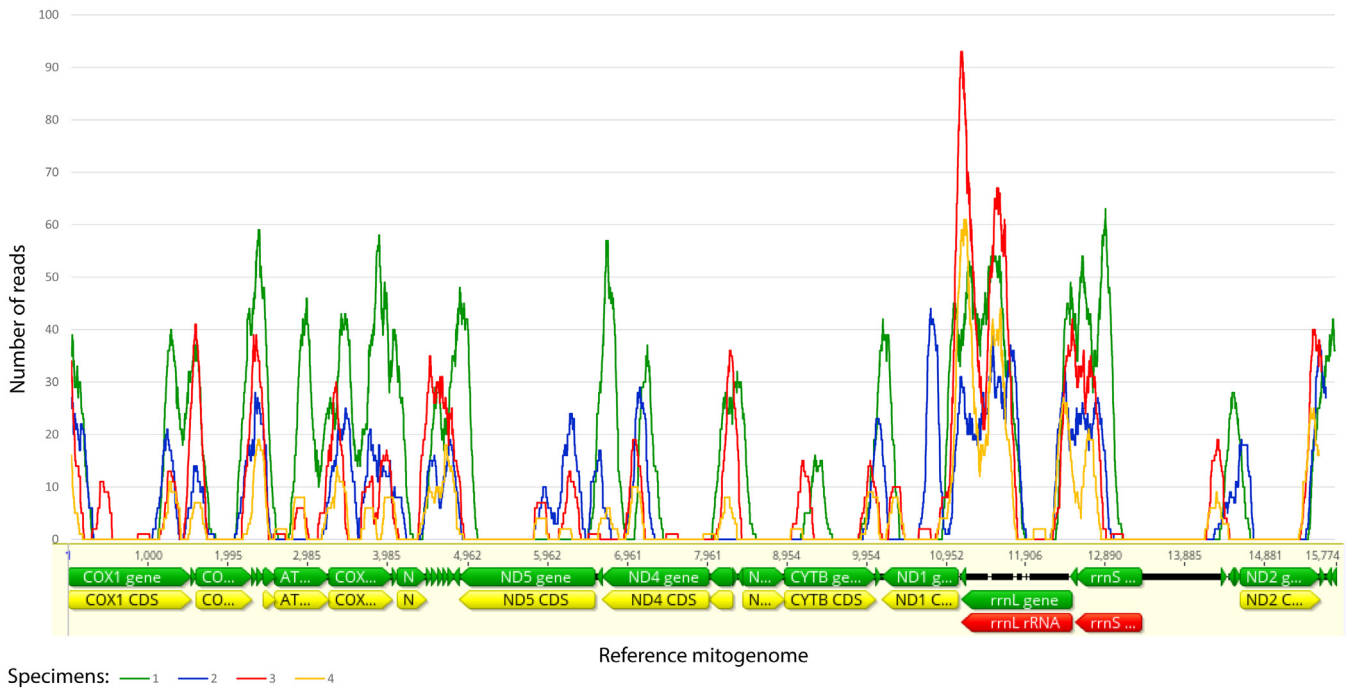


Fig. 2. Coverage graph of the number of reads mapped to each nucleotide position of the reference mitochondrial genome for each of the four specimens sequenced.

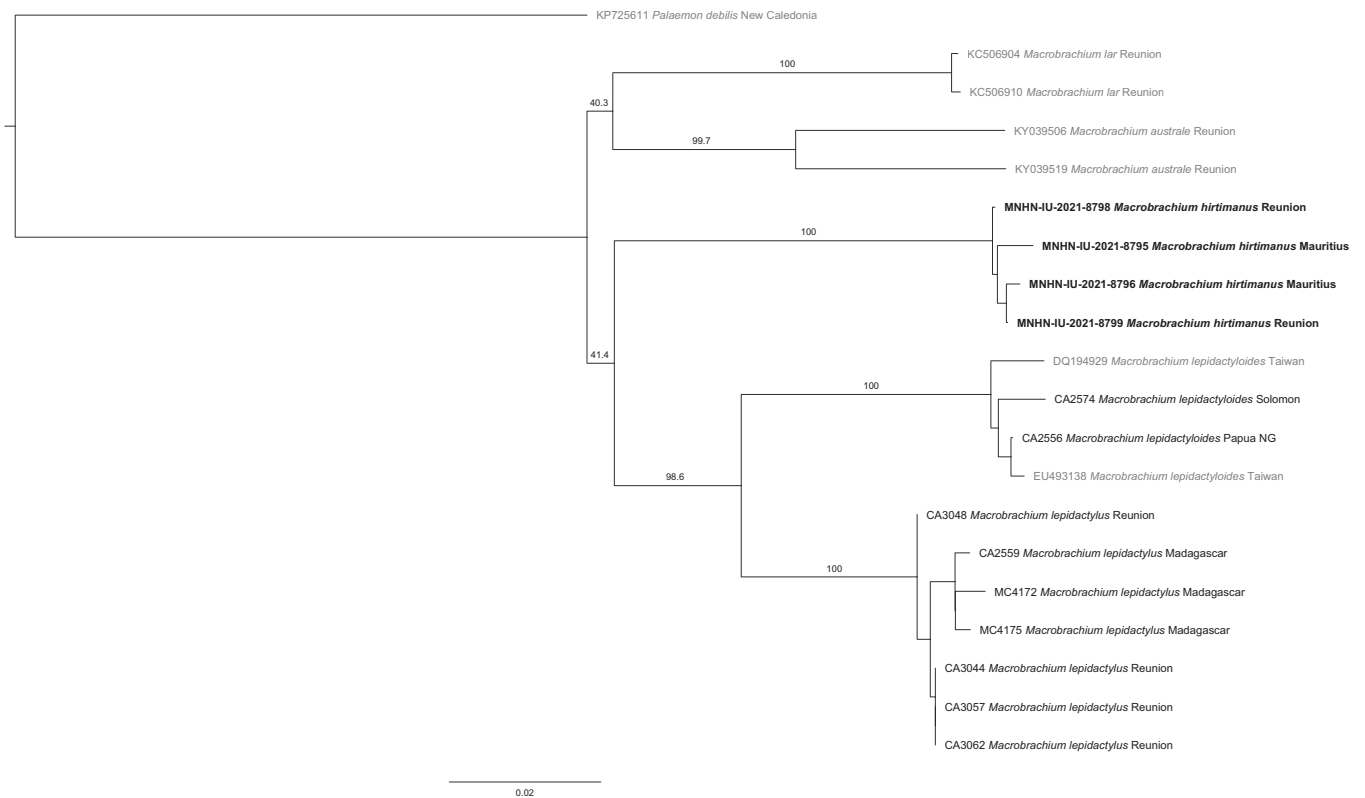


Fig. 3. Neighbor-Joining tree based on the 16S alignment.

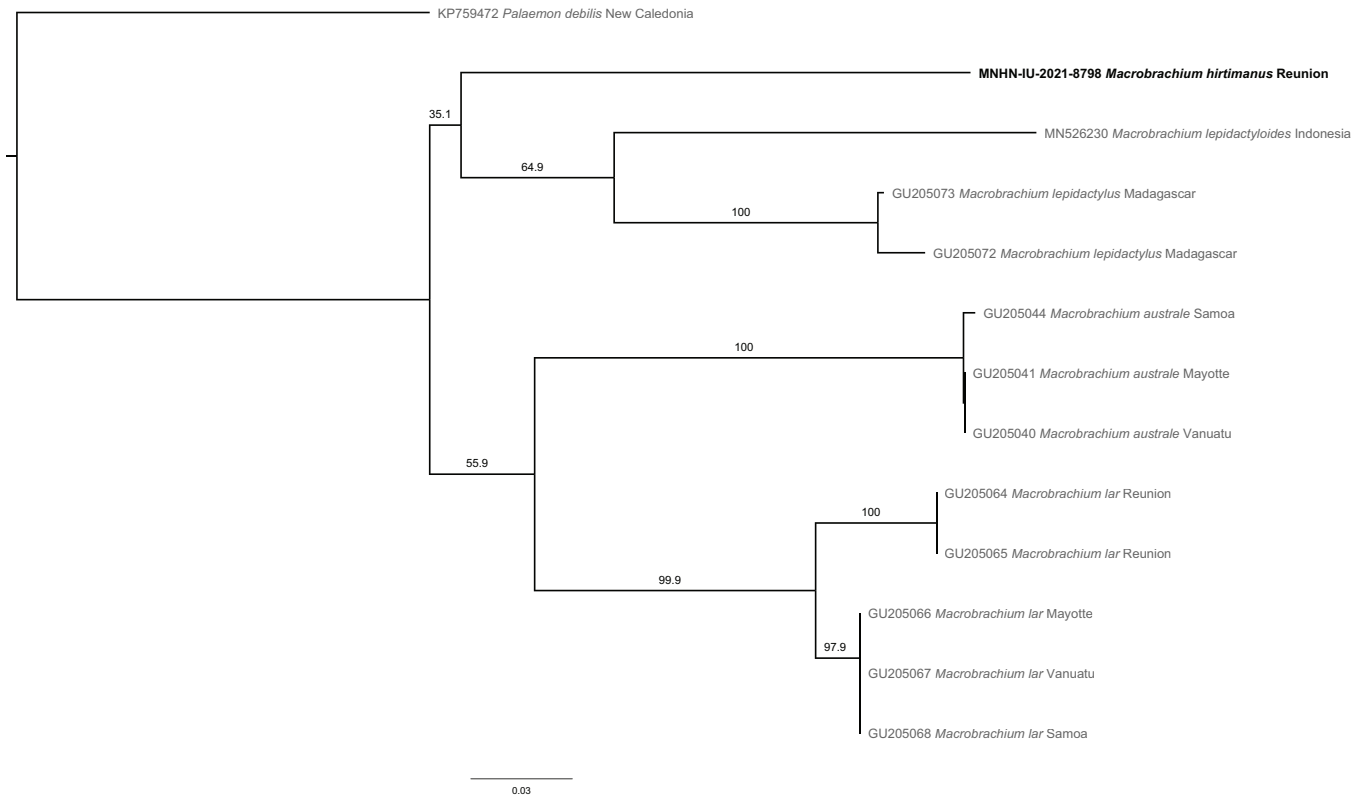


Fig. 4. Neighbor-Joining tree based on the COI alignment.

M. hirtimanus was caught. We now consider this specimen to be an immature *M. lepidactylus*. Later, [Keith and Vigneux \(2000\)](#) report their finding of adult specimens of the same species during prospections made in November 1998. In his book on the fauna of Mauritius, [F. Staub \(1993\)](#) illustrates his entry about *M. hirtimanus* with a colour photograph of an adult male individual that can clearly be identified as *M. lepidactylus*. These occurrences suggest that *M. lepidactylus* was already established in the Mascarenes by the early 1990s, while *M. hirtimanus* was last seen in 1980 ([Kiener and Duchochois, 1981](#)).

M. lepidactylus naturally occurs in East and South-East Africa, and Madagascar ([Holthuis, 1980](#)), living in well-oxygenated, flowing waters all along the river courses ([Keith and Vigneux, 2000](#)). It is unlikely for this species to have been introduced by man in the Mascarenes given its minor commercial interest ([Holthuis, 1980](#)). Since it is an amphidromous species ([Keith et al., 2006](#)) and due to the relative proximity of Madagascar, one can expect *M. lepidactylus* to reach Réunion and Mauritius Islands by natural means with post-larvae born in rivers of Madagascar recruiting in estuaries of these islands, drifting along favourable oceanic currents, as for other amphidromous species of the area (see [de Mazancourt et al., 2023](#); [Keith and Mennesson, 2023](#)).

However, why was it not present there before the 1990s? *M. hirtimanus* occupies the same habitat as *M. lepidactylus* ([Kiener pers. comm. in Keith and Vigneux, 2000](#)), which suggests that both species compete for the same ecological niche. Reduction in populations of *M. hirtimanus* in the 1980s due to poaching might have allowed juveniles of

M. lepidactylus to settle in favourable habitats where the presence of the well-established endemic species previously prevented it. Biological or ecological reasons explaining how *M. lepidactylus* might have outcompeted *M. hirtimanus* (e.g., more aggressive behaviour, life history traits, etc.) are yet to be found due to the lack of data on both species. This pattern is indeed very common in insular systems where ecologically plastic invasive species often supplant their endemic counterparts ([Russell et al., 2017](#)).

Compared to their marine counterparts, freshwater shrimps indeed face many threats specific to their inland habitat and migratory behaviour (see [De Grave et al., 2015](#); [de Mazancourt et al., 2021](#)). In the case of *M. hirtimanus*, poaching has been the main explanation ([Keith and Vigneux, 2000](#); [De Grave, 2013](#)) along with the degradation of its habitat ([Keith et al., 1999](#); [Keith, 2002](#); [De Grave, 2013](#)). Similarly, *Caridina natalensis* De Man, 1908, another freshwater shrimp native to the Mascarenes may be under threat of extirpation as it has become very rare on Réunion Island ([de Mazancourt et al., 2019b](#)) probably because of habitat degradation. On the other hand, old reports of a freshwater crab identified as *Potamon bouvieri* [Rathbun, 1904](#) from Mauritius ([Rathbun, 1904](#); [Jehangeer, 1984](#)) and Réunion ([Kiener and Duchochois, 1981](#)) should be investigated further as this species may also be extinct, if not just extremely rare.

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