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# A genetic snapshot before extinction: Museomics reveals the phylogenetic position of a critically endangered freshwater gastropod

Björn Stelbrink<sup>1</sup>  | Christian Kehlmaier<sup>2</sup>  | Catharina Clewing<sup>1</sup>  |  
Thomas Wilke<sup>1</sup>  | Christian Albrecht<sup>1</sup> 

<sup>1</sup>Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Giessen, Germany

<sup>2</sup>Museum of Zoology, Senckenberg Natural History Collections Dresden, Dresden, Germany

## Correspondence

Björn Stelbrink, Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26, 35392 Giessen, Germany.

Email: [bjorn.stelbrink@allzool.bio.uni-giessen.de](mailto:bjorn.stelbrink@allzool.bio.uni-giessen.de)

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## Abstract

Island species are particularly vulnerable to various anthropogenic impacts. Because several island endemics are rare and not accessible, obtaining genetic information and reconstructing their biogeographical and evolutionary history becomes increasingly difficult. In the present study, we investigated the endangered freshwater gastropod *Paludomus ajanensis* (family Paludomidae) endemic to the Seychelles (Mahé and Silhouette) in the western Indian Ocean. By analysing historical DNA of this species, we were able to place this species in the family Paludomidae and to uncover its Asian affinity. The patchy distribution plus the documented recent population decline suggests this species should be considered ‘Critically Endangered’.

## KEYWORDS

freshwater gastropods, museomics, oceanic islands, Paludomidae, phylogenetic inference, Seychelles

## 1 | INTRODUCTION

Insular systems, such as oceanic islands and archipelagos, often represent ‘biodiversity hotspots’ (e.g. Mittermeier et al., 2011). The peculiar biodiversity in these ecosystems has stimulated ecological and evolutionary research, including analyses of species-area relationships, equilibrium dynamics and biological invasions (see, e.g. Matthews & Triantis, 2021). However, recent anthropogenic factors, with habitat loss and the introduction of non-native species being the most severe, are exerting strong pressure on several locally restricted and vulnerable endemic island species (e.g. Bellard et al., 2017; Russell & Kueffer, 2019).

One of these biodiversity hotspots is the islands of the western Indian Ocean (WIOI), including Madagascar and smaller island archipelagos such as the Mascarene Islands, the Seychelles and the

Comoros (see Mittermeier et al., 2011). They are particularly renowned for their high endemism of plants and vertebrates (Mittermeier et al., 2011). In contrast, very little is known about the biodiversity, origin, diversification processes and threats of the freshwater fauna, except for some studies on crabs and diving beetles (see, e.g. Agnarsson & Kuntner, 2012). This bias towards plants and vertebrates, however, is unfortunate, because the global decline in the biodiverse freshwater invertebrates (e.g. Böhm et al., 2021) and the homogenization of the biota (e.g. Baiser et al., 2012) is likely to be even more pronounced in these less studied island systems. Nevertheless, the thorough investigation of freshwater invertebrate faunas in recent decades has provided a solid taxonomic backbone for many groups (see, e.g. Agnarsson & Kuntner, 2012 for an overview).

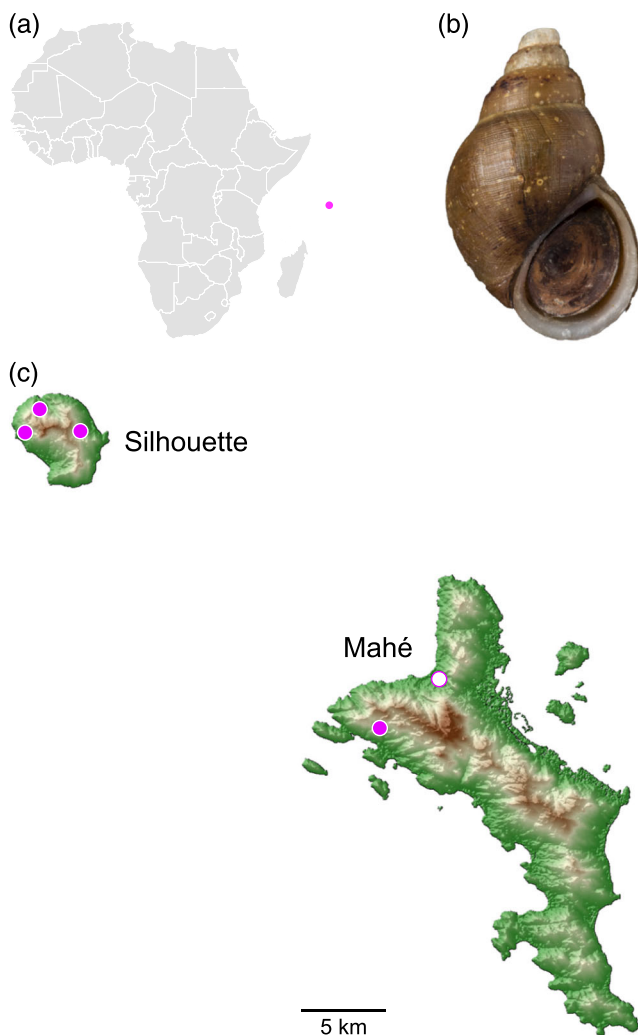
The WIOI form a heterogeneous meta-archipelago (Whittaker et al., 2018) comprising different types of islands (continental islands,

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oceanic islands and continental fragments; but see Ali, 2017 for a more detailed classification). They have different geological and palaeogeographical histories and ages and are inhabited by different floras and faunas (see, e.g. Agnarsson & Kuntner, 2012). However, only few groups have a rich (sub)fossil record to be exploited phylogenetically (see, e.g. Kehlmaier et al., 2019, 2023) and many species are endangered or even threatened with extinction. It is thus becoming increasingly difficult to link the evolutionary history of WIOI endemics to the geological history of their island of origin.

One example of this is the endemic gastropod *Paludomus ajanensis* Morelet, 1860. According to Gerlach (2006), this species only occurs on the Seychelles islands of Mahé (island size = 155 km<sup>2</sup>) and Silhouette (island size = 20 km<sup>2</sup>) in two and three populations, respectively, with about 25 individuals per population (Figure 1). However, in 2002, no



**FIGURE 1** Distribution of *Paludomus ajanensis* in its native range. (a) Location of the Seychelles (pink circle) in relation to the African continent. (b) The shell image refers to the syntype deposited at the Natural History Museum in London (cat. no. BMNH 1893.2.4.1525) that was probably collected at Ras Hafun, Somalia (see Brown & Gerlach, 1991 for a discussion on the type material). (c) Current distribution of *P. ajanensis*, with the pink circles indicating the five populations mentioned in Gerlach (2006). Note that the population at the Le Niol site on Mahé (white circle) has probably disappeared.

living specimens were found at the Le Niol site on Mahé, reducing the total population size from 125 to 100 individuals (Gerlach, 2006). Accordingly, the species has been considered 'Endangered' (Gerlach, 2006; Gerlach & Van Damme, 2016). Further attempts to find this (and other) gastropod species on Mahé and Praslin by several of the present authors in 2014, 2016 and 2017 were unsuccessful, questioning the continued existence of the only remaining population on that island.

The species belongs to the family Paludomidae, which comprises about 24 genera (Neiber & Glaubrecht, 2019) that are mainly restricted to the African continent. In contrast, most *Paludomus* species are confined to the Indian subcontinent and Indochina and represent the sister group to the African taxa (see Neiber & Glaubrecht, 2019). Morphological and anatomical features also support affinities to Asian conspecifics, although several authorities have suggested a closer relationship with African *Cleopatra* (see Brown & Gerlach, 1991 for a detailed discussion). The phylogenetic position of *Paludomus ajanensis* within the Paludomidae thus also has biogeographical implications as to whether the Seychelles were indeed colonized predominantly from the African continent and Madagascar (see the meta-analyses of Agnarsson & Kuntner, 2012; Bernardes et al., 2021) or whether its biota also shows Asian affinities, as has been revealed for a number of Malagasy species (Warren et al., 2010).

Our objectives are to (1) provide a genetic resource for an endangered, narrow-range endemic species that is likely threatened with extinction in the face of ongoing anthropogenic pressures; (2) place *P. ajanensis* in a phylogenetic context within the Paludomidae to better understand its biogeographical affinities; and (3) provide a preliminary re-assessment of the species' conservation status based on the known populations and their estimated sizes. Because genetic material from living specimens is not available, we apply a museomics approach here, isolating and sequencing historical DNA of material collected in 1989.

## 2 | METHODS

### 2.1 | Sample preparation and shotgun sequencing

Tissue samples of *P. ajanensis* were provided by the Natural History Museum, London (cat. no. BMNH:ETD 4259; Mahé, Le Niol District, small stream in secondary forest at about 250 m; coll.: Justin Gerlach, 17 September 1989; 10 specimens). Tissue was processed and historical DNA was isolated as recently described for other freshwater gastropods (Clewing et al., 2022; Stelbrink et al., 2019), though DNA extraction following a modified protocol of Straube et al. (2021). A total of 13.5 ng of DNA was used for single-indexed, single-stranded libraries, including the removal of uracil residues (see Stelbrink et al., 2019; Clewing et al., 2022 for details), and shotgun-sequenced (75 bp paired-end reads) on an Illumina MiSeq platform (San Diego, CA, USA) housed at the Senckenberg Natural History Collections Dresden (Germany).

## 2.2 | Mapping steps and phylogenetic analysis

Adapters were trimmed using Skewer 0.2.2 (Jiang et al., 2014), and reads were merged (min. length = 35 bp), filtered for quality (min. Q score = 20), and deduplicated using BBDuk 37.241 (Bushnell, 2014). This reduced readpool was then used for several mapping steps performed in Geneious Prime 2023.1.2 (<https://www.geneious.com>). In a first attempt, we aimed to map the readpool against the near-complete mitogenome of the paludomid gastropod *Pseudocleopatra dartavellei* (GenBank acc. no. MN082637; Stelbrink et al., 2019). For the mapping step, the Geneious mapper was used, with medium sensitivity and up to five iterations. Consensus sequences were generated with the threshold for highest quality = 60%, Sanger heterozygotes called >50%, and bases called '?' if coverage was <5. If long stretches of ambiguous sites were detected, the entire selection was converted to N, with a minimum distance between these stretches of 10 bp. Finally, genes from the published *P. dartavellei* mitogenome were annotated in Geneious Prime (similarity threshold = 50%).

Unfortunately, only very little genetic information is available for the Paludomidae, particularly with respect to nuclear DNA. However, we made use of a comprehensive mtDNA (COX1 and 16S) dataset compiled from Wilson et al. (2004); see also Stelbrink et al., 2019) and included three additional *Paludomus* samples available at GenBank, namely, *Paludomus siamensis* from Thailand (COX1 acc. no. MK094075, 16S acc. no.: MK098356; Wiggering et al., 2019), *Paludomus petrosus* from Myanmar (COX1 acc. no. MF983661; unpublished) and *Paludomus* sp. from India (COX1 acc. no. OR600529; unpublished). The 16S dataset was aligned using the MAFFT Web Service (Katoh & Standley, 2013) with default settings and trimmed to a final length of 519 bp. Both genetic datasets were combined (1,177 bp length) and subjected to IQ-TREE 2.2.0 (Minh et al., 2020), with GTR +  $\Gamma$  for both partitions and 10,000 UFboot replicates. Uncorrected genetic p-distances were calculated for the four available *Paludomus* COX1 sequences using MEGA X 10.1.7 (Kumar et al., 2018).

## 2.3 | Re-assessment of the conservation status

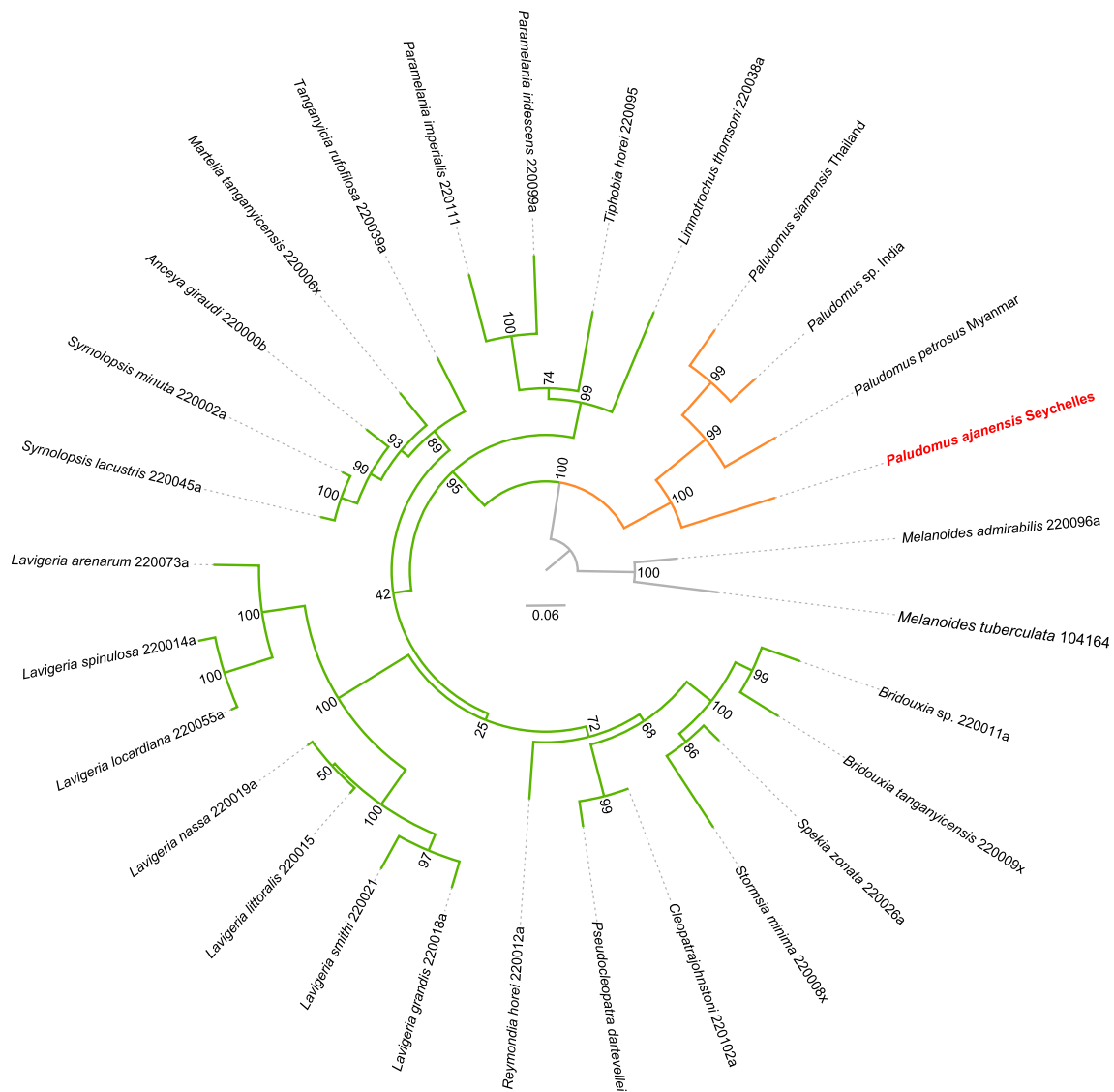
The conservation status of *P. ajanensis* was re-assessment based on the population information provided in Brown & Gerlach (1991) and Gerlach (2006). Accordingly, the estimated coordinates of the five populations (see Figure 1) were subjected to GeoCAT (<https://geocat.iucnredlist.org>; Bachman et al., 2011), applying a very conservative cell width of 1 km<sup>2</sup>, from which area of occupancy (AAO) and extent of occurrence (EOO) were calculated. The IUCN Red List criteria were used to make a final Red List assessment (IUCN, 2012) based on recent and past occurrences as well as small population size and decline (IUCN criteria B and C). The following localities were analysed: Mahé, Rivière Cascade, approx. -4.642876, 55.401545; Mahé, Le Niol, approx. -4.616667, 55.433333; Silhouette, Grande Rivière, approx. -4.483845, 55.241139; Silhouette, Rivière Macabee, approx. -4.472100, 55.219346; and Silhouette, west of Mt Dauban, approx. -4.484587, 55.211518.

## 3 | RESULTS AND DISCUSSION

The sequencing run yielded a total of 40,047,724 read pairs, of which 31,994,519 (79.9% of the raw read pairs) remained after adapter removal and only 10,409,086 (26.0% of the raw read pairs) after filtering and deduplication. Despite the low number of usable reads, a total of 225,221 reads were mapped against the mitogenome of *P. dartavellei*. As a result, a near-complete mitogenome of 15,055 bp length with a mean coverage of 5,185 could be generated (GenBank acc. no. PP946412). However, it also contains a comparatively high number of ambiguous sites ( $N_A = 3,715 = c. 24.7\%$ ,  $N_C = 2,164 = c. 14.4\%$ ,  $N_G = 2,388 = c. 15.9\%$ ,  $N_T = 4,430 = c. 29.4\%$ , and  $N_N = 2,358 = c. 15.7\%$ ), which made the annotation of several genes difficult.

The mtDNA phylogeny revealed a strongly supported ingroup, with *Paludomus* and the Lake Tanganyika flock (including several subclades) also highly supported (bootstrap values = 100 and 95, respectively; Figure 2). Within *Paludomus*, *P. ajanensis* is sister to the remaining species from India, Myanmar and Thailand, thus clearly indicating an Asian (rather than African) affinity for *P. ajanensis* as suggested by previous authorities (see Brown & Gerlach, 1991) and in contrast to the majority of WIOI taxa analysed (Agnarsson & Kuntner, 2012; Bernardes et al., 2021). *Paludomus ajanensis* probably diverged from the other species several million years ago, considering the comparatively large genetic p-distances for COX1 of 18.7%–19.1%. The Seychelles are a relatively old insular system that, along with India, separated from Madagascar between c. 90 and 85 Mya (Ali & Aitchison, 2008). Its geological age and proximity to these two landmasses allowed ancient colonization from various sources, including vicariant scenarios. However, given that the Seychelles were often completely submerged during their palaeogeographical history, it is highly likely that *P. ajanensis* and the remaining fauna colonized the islands primarily by dispersal (see, e.g. Agnarsson & Kuntner, 2012; Ali & Aitchison, 2008; Bernardes et al., 2021). However, it remains difficult to draw a final conclusion on phylogenetic relationships and biogeographical scenarios within the genus given that only four out of approx. 40 extant *Paludomus* species (see, e.g. Neiber & Glaubrecht, 2019) are included in the present phylogenetic tree, particularly lacking the two centres of diversity, India and Indochina.

In the latest IUCN assessment, the species was classified as 'Endangered', the total population of 100 individuals was considered stable, and the two island proper (Mahé and Silhouette) were marked as the species' native range (Gerlach & Van Damme, 2016). However, based on estimated point coordinates and a conservatively chosen cell width of 1 km<sup>2</sup>, calculated EOOs and AOOs were 89.2 and 5 km<sup>2</sup>, respectively, for all five populations and 32.1 and 4 km<sup>2</sup>, respectively, when the possibly extinct Le Niol (Mahé) population was excluded. In both cases, GeoCAT classifies *P. ajanensis* as 'Critically Endangered' [IUCN category B1a,b (iii) + B2a,b (iii)]. The same applies to further assessments of population sizes and population declines. Accordingly, the total number of mature individuals is less than 250, and a continuous



**FIGURE 2** Phylogenetic tree of Paludomidae based on the COI and 16S genes. The position of *Paludomus ajanensis* within the genus is highlighted in red. Asian lineages are coloured in orange, African lineages in green, and the outgroup (*Melanoidea* spp.) in grey. Collection numbers are provided for the samples from Lake Tanganyika (Africa) included in the dataset of Wilson et al. (2004).

decline is observed with less than 50 individuals remaining in each subpopulation [IUCN category C2a (i)]. The very few remaining populations and the documented population decline on Mahé from 1994 to 2002 (Gerlach, 2006) indicate that this phylogenetically ancient lineage has likely passed through a bottleneck, which may be ongoing given current anthropogenic pressures such as habitat loss and introduction of non-native species. We therefore propose changing the current conservation status from ‘Endangered’ to ‘Critically Endangered’. This may also raise awareness of the last remaining populations, especially the only one potentially left on Mahé.

This study highlights the importance of employing museomics for already extinct or vulnerable and protected species (see, e.g. Jensen et al., 2022). By analysing historical DNA derived from museum material, we were able not only to provide a genetic resource for this

‘Critically Endangered’ species but also to place it in a phylogenetic context that highlights the genetic distinctiveness of this island endemic within the genus and that will aid future studies investigating diversification patterns within the Paludomidae and reconstructing biogeographical histories within the WIOI.

#### AUTHOR CONTRIBUTIONS

**Björn Stelbrink:** Conceptualization; data curation; formal analysis; visualization (equal); writing—original draft preparation. **Christian Kehlmaier:** Data curation; formal analysis; resources; writing—review and editing. **Catharina Clewing:** Formal analysis; visualization (equal); writing—review and editing. **Thomas Wilke:** Funding acquisition; supervision (equal); writing—review and editing. **Christian Albrecht:** Conceptualization; formal analysis; supervision (equal); writing—review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

All data generated or analysed in this study are included in the article or available from the corresponding author on request. The newly mitogenome was submitted to the NCBI GenBank database under the accession number PP946412.

## ETHICS STATEMENT

The first author signed a CETAF (Consortium of European Taxonomic Facilities) agreement with Jonathan Ablett and Muriel Rabone (Natural History Museum, London, UK) to use the museum material for the present genomic analyses.

## ORCID

Björn Stelbrink  <https://orcid.org/0000-0002-7471-4992>

Christian Kehlmaier  <https://orcid.org/0000-0001-9622-0566>

Catharina Clewing  <https://orcid.org/0000-0001-7974-5037>

Thomas Wilke  <https://orcid.org/0000-0001-8263-7758>

Christian Albrecht  <https://orcid.org/0000-0002-1490-1825>

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