Review of threatened Malagasy freshwater fishes in zoos and aquaria: The necessity of an ex situ conservation network—A call for action

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Abstract
Madagascar’s biota is characterized by an extraordinary species richness, with a high degree of endemism. The island’s freshwater habitats harbor numerous micro-endemic species, restricted to particular regions and thus particularly at risk of extinction, due to deforestation, overfishing, and introduction of exotic species. The present study investigates for which threatened Malagasy freshwater fish species ex situ populations have already been established, as a baseline to prioritize actions to develop an effective ex situ conservation breeding network. Populations in zoos and aquaria were primarily determined using the Zoological Information System. Of 173 fish species recorded from Malagasy freshwater habitats, 123 exclusively inhabit freshwater; 79 of these are endemic to Madagascar, and 50 are classified as threatened. Our survey found 21 Malagasy freshwater fish species kept in zoos worldwide, of which 19 are endemic and threatened (22 if counting species kept by private breeders). Nine of the 19 Malagasy freshwater fish species kept in zoos have successfully reproduced within the 12 months preceding our survey. The ex situ conservation activities for threatened Malagasy freshwater fishes thus have not improved significantly since the strong start in the early 2000s. More than half of the 50 threatened endemic Malagasy freshwater fish species (viz. 31 species) are not kept ex situ, including 11 species ranked as Critically Endangered. Based on these findings we call for a better distribution of offspring among institutions, including private breeders in the framework of citizen conservation initiatives; a closer connection of ichthyological field research in Madagascar with conservation breeding efforts to set up ex situ populations—both in Madagascar and abroad—of species not yet kept in captivity; and the development of effective, integrated in situ and ex situ conservation strategies.

Keywords
aquatic vertebrates, conservation breeding, Madagascar
1 | INTRODUCTION

Madagascar, the world’s fourth largest island and situated in the Indian Ocean (Benstead et al., 2003), has probably been isolated from any other land masses for the last 88 million years (Ali & Huber, 2010; Ali & Vences, 2019), despite recurrent speculations about subaerial terrestrial causeways in the Cenozoic (Masters et al., 2020).

As a result of this isolation, Madagascar has a unique flora and fauna characterized by a high level of endemism. Nearly 90% of all animal and plant species found are endemic (Goodman & Benstead, 2003). Madagascar also offers a large variety of biomes characterized by distinct climatic conditions conducive to micro-endemism, viz. organisms whose populations are limited to a small habitat area only, e.g., a single lake, a tiny rock island or mountain, or a short river section (Ganzhorn et al., 2016; Wilmé et al., 2006). These micro-endemic species are particularly threatened by extinction because their habitats are being destroyed quickly, often before conservation measures can become effective (Passal, 2015). Based on the criteria of Myers et al. (2000), such as diversity of species, endemism, and loss in habitat, Madagascar has been recognized as a global hotspot for biodiversity conservation (Ganzhorn et al., 2008; Groombridge & Jenkins, 1998).

Human colonization of Madagascar has been hypothesized to be older than 10,000 years (Anderson et al., 2018). Other studies point at the presence of humans at the island from about 3500 years before present (Anderson et al., 2018), which is shortly before the island’s biodiversity became substantially affected (e.g., Burney et al., 2003). As a consequence, the local vegetation has been lost in large parts of the central highland (Benstead et al., 2003; Ganzhorn et al., 2016; Harper et al., 2007). In total, Lowry et al. (1997) estimated a habitat loss of 90%. Human interventions have also negatively affected all freshwater habitats, mainly through the combination of overfishing, deforestation, and introduction of neozoans (exotic species). As a consequence, freshwater fishes can be considered as the most threatened vertebrates of Madagascar (Benstead et al., 2003; Taylor 1986).

Of the 143 fish species listed by Sparks and Stiassny (2003), all those that complete their entire life cycle in fresh water—over 65%—are endemic, and many of them also micro-endemic. Malagasy freshwater fishes are phylogenetically often splitting from relatively basal nodes in their respective clades in the actinopterygian tree (Benstead et al., 2003) and thus are evolutionary unique (Stiassny & de Pinna, 1994).

According to Benstead et al. (2003), 22% of Madagascar’s freshwater fishes assessed at the time were Critically Endangered, 34% Endangered, 17% Vulnerable, 5% Near Threatened and 4% already Extinct, using criteria established by the International Union for Conservation of Nature and Natural Resources (IUCN, 2001). Habitat conservation measures are urgently required to prevent further extinctions, but for many species, ex situ captive breeding at this time represented the only reliable means to save them from extinction (Benstead et al., 2003; Loiselle, 2003). In this context, it was and is obvious that zoos, being important conservation centers with global network activities, have the potential to contribute by preserving viable populations of species threatened with extinction due to the increased loss of habitats in the wild (Conde, 2013; Wayre, 1969).

Eighteen years after the studies of Benstead et al. (2003) and Loiselle (2003), we aimed to assess which threatened Malagasy freshwater fish species ex situ populations have been built up, and to use this information to prioritize actions to develop an effective ex situ conservation breeding network supportive to in situ fish conservation measures (Conde, 2013). For this purpose, we surveyed holdings in zoos and aquaria, tabulating the number of species kept, the number of individuals per species, the number of institutions keeping a species, and those with breeding success over the last 12 months, from the Zoological Information Management System (ZIMS: Species360). These surveys were performed at a global scale but focusing on Europe as a regional example. The ZIMS data were supplemented with data from the database List of Zoo Animals (ZTL). In addition, a preliminary survey was initiated to include private holdings of threatened Malagasy freshwater fishes. Based on these findings we provide a call for action and have drafted a commentarial guide.

2 | MATERIALS AND METHODS

A list of Malagasy freshwater fish species was compiled based on the database FishBase (Froese & Pauly, 2019). Only scientifically named species were considered. Based on the World Register of Marine Species (WoRMs Editorial Board, 2020), 46 species were designated as not exclusively occurring in freshwater. They were marked in Table 1 (e.g., the sharks Carcharhinus amboinensis, C. leucas) but then excluded from further analyses.

Fish species were classified as “introduced” (i.e., not naturally occurring in Madagascar), “native” (naturally occurring in Madagascar but also elsewhere) and “endemic” (naturally occurring and only found in Madagascar). The status of introduced species was cross-checked with information from FAO Fisheries and Aquaculture Department (2017), and these species (see Table 1) were excluded from all further analyses. Additionally, the conservation status and population trend of each species according to IUCN (2020) was added. The distribution data were compared with Froese and Pauly (2019) and the range completed, if necessary. The endemic species were further sub-classified into occurring nationwide (endemic), only regionally but occurring in more than one site (e.g., more than one river section) (regionally endemic), or at one restricted site only (e.g., limited to one river section or basin) (micro-endemic).

In addition, information on the IUCN (2020) threat status was collected. The species categorized by IUCN (2020) as Vulnerable (VU), Endangered (EN) and Critically Endangered (CR), were considered as “threatened” in this analysis. Additional threat categories were Extinct (EX), Near Threatened (NT), Data Deficient (DD), Not Evaluated (NE) and Least Concern (LC).

To gain an overview of native Malagasy freshwater fish species globally held in zoos, the number of individuals kept, the number of
### Table 1: Fish species reported from Malagasy freshwater habitats (n = 173), alphabetically sorted by family, including source, conservation status, population trend (IUCN, 2020), records in ZIMS and/or ZTL

| Family     | Species               | Source | IUCN status | Pop. trend | ZIMS | ZTL |
|------------|-----------------------|--------|-------------|------------|------|-----|
| Ambassidae | *Ambassia ambassis*   | Nat    | LC          | ?          |      |     |
|            | *A. fontoyonti*       | End    | DD          | ?          |      |     |
|            | *A. gymnnocephalus*   | Nat    | LC          | ?          |      |     |
| Ambassidae | *A. natalensis*       | Nat    | LC          | ?          | x    |     |
|            | *A. urotaenia*        | Nat    | LC          | —          |      |     |
| Anabantidae| *Microctenopoma ansorgii* | Int | LC          | ?          | x    |     |
| Anchariidae| *Ancharius fuscus*    | End    | LC          | ?          |      |     |
| Anchariidae| *A. griseus*          | End    | EN          | ?          |      |     |
| Anchariidae| *Gogo arcuatus*       | End    | DD          | ?          |      |     |
| Anchariidae| *G. atratus*          | End    | DD          | ?          |      |     |
| Anchariidae| *G. brevibarbis*      | End    | DD          | ?          |      |     |
| Anchariidae| *G. ornatus*          | End    | EN          | ?          |      |     |
| Anguillidae| *Anguilla bicolor*    | Nat    | NT          | ?          |      |     |
| Anguillidae| *A. labiata*          | Nat    | LC          | ?          |      |     |
| Anguillidae| *A. marmorata*        | Nat    | LC          | ?          | x    |     |
| Anguillidae| *A. mossambica*       | Nat    | NT          | ?          |      |     |
| Aplocheilidae| *Pachypanchax amoulti* | End | VU          | ↓ X X      |      |     |
| Aplocheilidae| *P. omonotus*        | End    | EN          | ↓ X X      |      |     |
| Aplocheilidae| *P. patriciae*       | End    | EN          | ? X        |      |     |
| Aplocheilidae| *P. sakaramyi*       | End    | EN          | ↓ X X      |      |     |
| Aplocheilidae| *P. sparksorum*      | End    | EN          | ↓ X        |      |     |
| Aplocheilidae| *P. varatara*        | End    | EN          | ? X        |      |     |
| Apogonidae  | *Fibramia lateralis*  | Nat    | LC          | ?          |      |     |
| Arapaimidae| *Heterotis niloticus* | Int    | LC          | ? X        |      |     |
| Ariidae     | *Arius africanus*     | Nat    | DD          | ?          |      |     |
|            | *A. festinus*         | End    | CR          | ↓          |      |     |
| A ridae     | *A. madagascariensis* | Nat    | LC          | ?          |      |     |
| A ridae     | *A. uncinatus*        | End    | CR          | ↓          |      |     |
| A ridae     | *Plicofolis dussumieri* | Nat | LC          | —          |      |     |

### Table 1 (Continued)

| Family     | Species               | Source | IUCN status | Pop. trend | ZIMS | ZTL |
|------------|-----------------------|--------|-------------|------------|------|-----|
| Atherinidae| *Teramulus kieneri*   | End    | LC          | ?          |      |     |
|            | *T. waterloti*        | End    | EN          | ↓          |      |     |
| Bedotiidae | *Bedotia albomarginata* | End | EN          | ?          |      |     |
| Bedotiidae | *B. alveyi*           | End    | NT          | ?          |      |     |
| Bedotiidae | *B. geayi*            | End    | EN          | ↓ X X      |      |     |
| Bedotiidae | *B. leucopteront*     | End    | EN          | ?          |      |     |
| Bedotiidae | *B. longianalis*      | End    | EN          | ? X        |      |     |
| Bedotiidae | *B. madagascariensis* | End    | EN          | ↓ X X      |      |     |
| Bedotiidae | *B. marojezy*         | End    | EN          | ↓ X        |      |     |
| Bedotiidae | *B. masaola*          | End    | VU          | ?          |      |     |
| Bedotiidae | *B. tricolor*         | End    | CR          | ?          |      |     |
| Rhexocles alaoentoensis* | End | EN          | ↓          |      |     |
| Rhexocles alaoentoensis* | End | CR          | ↓          |      |     |
| Rhexocles alaoentoensis* | End | DD          | ?          |      |     |
| Rhexocles alaoentoensis* | End | EN          | ↓ X X      |      |     |
| Carcharhinidae| *Carcharhinus amboinensis* | Nat | DD          | ?          |      |     |
| Carcharhinidae| *C. leucas*          | Nat    | NT          | ? X        |      |     |
| Centrarchidae| *Lepomis macrochirus* | Int    | LC          | — X        |      |     |
| Channidae   | *Chanos chanos*       | Nat    | LC          | ? X        |      |     |
| Channidae   | *Channa maculata*     | Int    | LC          | ?          |      |     |
| Cichlidae   | *Cichlasoma stryiata* | Int    | LC          | ? X        |      |     |
| Cichlidae   | *Coptodon rendalli*   | Int    | LC          | ? X        |      |     |
| Cichlidae   | *C. zillii*           | Int    | LC          | ?          |      |     |
| Cichlidae   | *Katria katria*       | End    | EN          | ↓          |      |     |
| Cichlidae   | *Oreochromis aureus*  | Int    | LC          | ? X        |      |     |
| Cichlidae   | *O. macrochir*        | Int    | VU          | ? X        |      |     |
| Cichlidae   | *O. mossambicus*      | Int    | NT          | ? X        |      |     |
| Cichlidae   | *O. niloticus*        | Int    | LC          | ? X        |      |     |
| Family          | Species                      | Source | IUCN status | Pop. trend | ZIMS | ZTL |
|-----------------|------------------------------|--------|-------------|-----------|------|-----|
| **Oreochromis spilurus** | Int | LC | ? |
| **Oxylapia polli** | End | EN | ? |
| **Paratilapia polleni** | End | VU | ↓ | x | x |
| **Pareptopus dambabe** | End | CR | ↓ |
| **P. damii** | End | VU | ? | x | x |
| **P. gymnopleorpercularis** | End | CR | ↓ |
| **P. kieneri** | End | VU | ? | x | x |
| **P. lamabane** | End | EN | ? |
| **P. loisellei** | End | EN | ? | x |
| **P. maculatus** | End | CR | ↓ | x | x |
| **P. maromandia** | End | EN | ↓ |
| **P. menarambo** | End | EN | ? | x | x |
| **P. nourissati** | End | DD | ? |
| **P. polyactis** | End | LC | ↓ |
| **P. tsimoly** | End | EN | ↓ |
| **Ptychochromis curvidens** | End | DD | ? |
| **P. ernestmagnusi** | End | DD | ? |
| **P. grandidieri** | End | LC | ? | x | x |
| **P. inornatus** | End | EN | ↓ |
| **P. insolitus** | End | CR | ↓ | x | x |
| **P. loisellei** | End | EN | ↓ | x |
| **P. mainy** | End | DD | ? |
| **P. makira** | End | DD | ↓ |
| **P. oligacanthus** | End | EN | ↓ | x |
| **P. onilany** | End | EX | ? |
| **Ptychochromoides betiseanu** | End | CR | ? |
| **P. itasy** | End | CR | ? |
| **P. vondrozo** | End | EN | ? |
| **Tilapia sparmanii** | Int | LC | ? | x |
| **Clupeidae** | **Sauvagella madagascariensis** | End | LC | ? |
| **Sauvagella robusta** | End | EN | ? |
| **Cyprinidae** | **Carassius auratus** | Int | LC | ? | x |
| **Cyprinus carpio** | Int | VU | ? | x |
| **Labeo rohita** | Int | LC | ? |

(Continues)
keeping institutions, and successful reproduction within the last 12 months were analyzed based on information collected from ZIMS (https://zims.species360.org) database in spring 2020. The ZIMS list may miss some captive populations or breeding records, as some data may be obsolete or have not (yet) been entered in the database, and some zoos do not use ZIMS. To increase the coverage of our data set, we additionally cross-checked the ZIMS data with species holdings for further institutions in Germany and Europe recovered from the website “Zootierliste” (ZTL, List of Zoo Animals: https://zootierliste.de/) which includes holdings of additional institutions as well as some private zoos, rescue stations and other facilities (Graf et al., 2019). ZTL data were only analysed in our overall summary of species present in holdings as for most ZTL data the last entries date back to 4 years ago and thus are of limited relevance when quantifying current animal stocks.

### TABLE 1 (Continued)

| Family | Species | Source | IUCN status | Pop. trend | ZIMS | ZTL |
|--------|---------|--------|-------------|------------|------|-----|
| Stenogobius genivittatus<sup>+</sup> | Nat | LC | ? |
| S. polyzona | Nat | LC | ? |
| Taenioides gracilis | Nat | LC | ? |
| Haemulidae | Plectorhinchus gibbosus<sup>+</sup> | Nat | LC | – |
| Kraemeriidae | Gobitrichinotus arnoulti | End | LC | ? |
| Kuhlidae | Kuhlia caudavittata<sup>+</sup> | Nat | NE |
| K. mugii<sup>+</sup> | Nat | LC | ? x |
| K. rupestris<sup>+</sup> | Nat | LC | – |
| K. sauvagii | End | VU | – |
| Megalopidae | Megalops cyprinoides<sup>+</sup> | Nat | DD | ? x |
| Milyeringidae | Typhleotris madagascariensis | End | EN | ? |
| T. mararybe | End | CR | – |
| T. pauliani | End | CR | ? |
| Mugilidae | Agonostomus catalai<sup>+</sup> | Nat | DD | ? |
| A. telfairii | Nat | LC | ? |
| Mugil cephalus<sup>+</sup> | Nat | LC | – x |
| Planiliza alata<sup>+</sup> | Nat | LC | ? |
| P. macrolepis<sup>+</sup> | Nat | LC | – |
| P. melinopterus<sup>+</sup> | Nat | LC | ? |
| Opichthidae | Pisodonophis boro<sup>+</sup> | Nat | LC | ? |
| P. cancrivorus<sup>+</sup> | Nat | NE |
| Osphronemidae | Macropodus opercularis | Int | LC | ↓ x |
| Osphronemus goramy | Int | LC | – x |
| Poeciliidae | Gambusia affinis | Int | LC | – x |
| G. holbrooki | Int | LC | – x |
| Pantanodon madagascariensis | End | EX | ? |
| Poecilia reticulata | Int | NE | x |
| Xiphophorus hellerii | Int | LC | – x |
| Xiphophorus maculatus<sup>+</sup> | Int | DD | ? x |
| Pristidae | Pristis microdon<sup>+</sup> | Nat | NE |
| Pristigasteridae |PELLONA JITCHELA<sup>+</sup> | Nat | LC | ? |
| Salmonidae | Oncorhynchus mykiss | Int | NE | x |
| Scatophagidae | Scatophagus tetracanthus<sup>+</sup> | Nat | LC | – |
| Sillaginidae | Silago sihama<sup>+</sup> | Nat | LC | – x |
| Sparidae | Acanthophagus berda<sup>+</sup> | Nat | LC | ? |
| Syngnathidae | Hippichthys cyanospilos<sup>+</sup> | Nat | NE |
| Microphis brachyrurus<sup>+</sup> | Nat | LC | ? x |
| M. fluviatilis<sup>+</sup> | Nat | DD | ? |
| M. leiaspis<sup>+</sup> | Nat | LC | ? |
| M. millepunctatus<sup>+</sup> | Nat | NE |
| Terapontidae | Mesopristes elongatus | End | DD | ? |
| Terapon jarbua<sup>+</sup> | Nat | LC | ? x |

Note: Nat = native (nonendemic); End = endemic; Int = introduced; + = freshwater, brackish water and marine; ↓ = decreasing; – = stable. Abbreviation: ZIMS, Zoological Information System.
For the analysis, all countries that geographically belong to the European continent were considered as “Europe”. Moreover, as over 20% of Russia’s land surface is located on the European continent, figures of Russian zoos were included in the ZIMS analyses as well.

To collect preliminary information about private fish holdings of Malagasy freshwater fishes, a questionnaire was developed and sent in June 2020 both to the Deutsche Cichliden-Gesellschaft e.V. (German Cichlid Society) and to the administrator of the Facebook group “Madagascar Endangered Fishes.”

3 | RESULTS

3.1 | Species diversity and threat evaluation

A total of 173 fish species representing 35 different families are currently reported to occur in Malagasy freshwater habitats (Froese & Pauly, 2019); 123 of them are restricted to pure freshwater (see Table 1), in the following referred to as Malagasy freshwater fish species. Cichlids, with 37 species, are the most diverse Malagasy freshwater fish family, followed by bedotiids (37 species). Of the 123 species, 26 are introduced (21%), and 97 are native (79%). Of the native species, 79 are endemic (64%; Figure 1). All species of the families Bedotiidae (16), Anchariidae (6) and Aplocheilidae (6) are endemic to Madagascar. Among all cichlids occurring in Madagascar, 29 species (78%) are endemic, the other eight species (22%) are introduced.

According to IUCN (2020), more than half of Madagascar’s native freshwater fish species are threatened (50 of 97 species). Fifty of the 79 endemic Malagasy freshwater fish species (63%) are threatened (Figures 1 and 2; Table 2). Of the 79 endemic freshwater fish species, 16 are micro-endemic (Table 3), with 13 of them being threatened; and four are regionally endemic (Table 4), all of them being threatened. The 29 endemic Malagasy freshwater fish species which are not listed as threatened correspond to the categories Data Deficient or Not Evaluated. Two species, Pantanodon madagascariensis and Ptychochromis onilahy are considered as Extinct. Most of the threatened species (60%) are listed as Endangered. The population trend is declining in 37% of the endemic freshwater fish species. For 50 endemic Malagasy freshwater fish species (63%), the extent of population decline is unknown. Only for one of the species listed as Data Deficient or Not Evaluated, a population trend was indicated (Ptychochromis makira, with population declining).

4 | ZIMS ANALYSIS

4.1 | Malagasy freshwater fish species globally held in zoos

According to ZIMS 20 native Malagasy freshwater fish species are globally held in zoos. In total, they account for 4267 individuals (Figure 3). The vast majority of these (19 of 20 species; 4262 individuals) are Madagascar-endemics and about 90% of the species (18 species; 2972 individuals) are threatened. The native species Anguilla marmorata (represented by a population of five captive individuals) and the endemic species Ptychochromis grandidieri (1290 captive individuals) are not threatened and listed as Least Concern by the IUCN (2020) (see Table 1).

4.2 | Malagasy freshwater fish species held in zoos by continents

The highest numbers of Malagasy freshwater fish species are held in North American zoos (16 species) and European zoos (15 species), with very few records from Asian and South American zoos.

The 16 species held in North American zoos are represented by three families: Bedotiidae (four species), Cichlidae (nine species) and Aplocheilidae (three species) (see Figure 4). All of these species are endemic to Madagascar, with Bedotia geayi being the most common species (with 201 individuals). However, many if not all of these records may in fact represent Bedotia madagascariensis.
(see Section 5.3). The B. geayi records are followed by Rheocles vatosoa (with 81 individuals). Paretroplus loisellei and Ptychochromis oligacanthus are the rarest species held in North American zoos.

The 15 species held in European zoos are likewise represented by the same three families: Bedotiidae (four species), Cichlidae (eight species) and Aplocheilidae (three species) (see Figure 6). Ptychochromis grandidieri is the most common species in Europe, with in total 1283 held individuals, followed by Pachypanchax sakaramyi with 510 individuals, and Paratilapia polleni (345 individuals). Bedotia longjanalis represents the rarest species held in a European zoo.

**FIGURE 2** Threat status of Malagasy freshwater fish species (in %) after IUCN (2020): (a) all species (n = 97); (b) endemic species (n = 79); absolute species numbers in parentheses. CR, critically endangered; DD, data deficient; EN, endangered; EX, extinct; LC, least concern; NE, not evaluated; NT, near threatened; VU, vulnerable

**TABLE 2** Threat evaluation of native and endemic Malagasy freshwater fish species, respectively; in brackets endemic species with declining population trend (after IUCN, 2020)

| IUCN category | Native species: 97 | Endemic species: 79 (29) | Micro-endemic species: 16 (10) |
|---------------|--------------------|--------------------------|-------------------------------|
| Threatened    |                    |                          |                               |
| Critically Endangered (CR) | 14 | 14 (6) | 7 (6) |
| Endangered (EN) | 30 | 30 (17) | 5 (3) |
| Vulnerable (VU) | 6 | 6 (2) | 1 (?) |
| Other categories |                    |                          |                               |
| Extinct (EX) | 2 | 2 (−) | 0 (−) |
| Near Threatened (NT) | 3 | 1 (0) | 0 (−) |
| Least Concern (LC) | 22 | 9 (1) | 0 (−) |
| Data Deficient (DD) | 17 | 15 (1) | 3 (1) |
| Not Evaluated (NE) | 3 | 2 (?) | 0 (−) |
In Asia, the native, nonthreatened *Anguilla marmorata* (Anguillidae) is the only species held. It is not probable that the five individuals kept originate from Malagasy populations.

Also, in South America only one species is held, *Bedotia geayi* (Bedotiidae), with a single individual reported.

### 4.3 Malagasy freshwater fish species held in zoos in Europe

A total of 14 of the 15 Malagasy freshwater fish species held within European zoos are listed as threatened by IUCN (2020). This represents 2319 individuals, three times the number of threatened individuals held outside of Europe (653). However, there is a slightly greater number of different species (16) held outside Europe than in Europe (14).

Within Europe, most of the Malagasy freshwater fish species are held in Germany (see Figure 5). 11 of the 12 species kept in Germany are listed as threatened by IUCN (2020). A total of 744 out of 749 (99%) of the individuals kept in Germany belong to threatened species. Most threatened Malagasy freshwater fish species (n = 7) are held at the Cologne Zoo, followed by Aquazoo in Düsseldorf (n = 4).

In United Kingdom, 10 threatened Malagasy freshwater fish species are held in zoos, followed by Czech Republic (seven threatened species) and the Netherlands and Switzerland (each with five threatened species).

The family Bedotiidae is represented by five species in European zoos. *Bedotia geayi* is kept in seven European countries (see Figure 6); however, these may in fact represent *B. madagascariensis*, which explicitly is kept in five European countries. *Rheocles vatosoa* is kept only in Germany and in United Kingdom with few individuals. *Bedotia longianalis* is only kept in Czech Republic, with one individual (see Figure 6).

The family Cichlidae is represented by eight species in European zoos. *Paratilapia polleni* and *Paretroplus menarambo* are kept in most countries on the European continent (n = 7), followed by *Paretroplus*...
FIGURE 3  Number of Malagasy freshwater fish individuals ($n = 4267$) globally held in zoos (bars coloured according to family; * = endemic species; NT = nonthreatened species), after ZIMS. ZIMS, Zoological Information System.

FIGURE 4  Number of Malagasy freshwater fish individuals held in North American ($n = 659$) and European ($n = 3602$) zoos (NT = nonthreatened species; * = endemic species)
kieneri (kept in six countries). Ptychochromis insolitus is held in four countries, with the largest group being held in Germany. The endemic but nonthreatened Ptychochromis grandidieri is held in three countries, with highest individual numbers (1178) in Denmark (in a single institution). Paretroplus damii is held in two countries, with 35 individuals in United Kingdom and eight individuals in the Netherlands. Ptychochromis loisellei was only kept at the Cologne Zoo in Germany a few years ago until offspring was distributed from there to other zoos (Ziegler et al., 2020) (see Figure 6).

The family Aplocheilidae is represented by three species in European zoos. Pachypanchax sakaramyi is kept in eight countries, followed by Pachypanchax omalonotus (kept in six countries). Pachypanchax arnouti is kept only in two institutions, one in Germany (Aquazoo Düsseldorf, 30 individuals) and one in United Kingdom (ZSL London Zoo, 20 individuals) (see Figure 6).

4.4 | Reproduction success

According to ZIMS, a total of ten out of the 20 globally zoo-kept Malagasy freshwater fish species successfully reproduced within the 12 months preceding our survey (see Table 5). All of the 10 species, distributed among three families, were both endemic and threatened. In North America, six species successfully reproduced (Pachypanchax arnouti, Pachypanchax sakaramyi, Bedotia geayi, B. marojey, Paretroplus kieneri, P. loisellei). In Europe, nine species successfully reproduced (Bedotia geayi, B. madagascariensis, Rheocles vatosoa, Pachypanchax arnouti, Pachypanchax omalonotus, Pachypanchax sakaramyi, Paretroplus kieneri, Ptychochromis insolitus, and Ptychochromis loisellei), with Ptychochromis insolitus and P. loisellei having bred for the first time in zoos in Europe (Ziegler et al., 2020). However, de Rham and Nourissat (2002) reported about their breeding of Pt. "de Mandrisitsara" (sic), which might apply (due to the region of Mandritsara) to another breeding success of P. insolitus, this time in a private facility.

5 | ZTL ANALYSIS

According to ZTL a total of 15 Malagasy freshwater fish species are held in zoos in Europe. All 15 species are endemic to Madagascar. A total of 13 of them are listed both in ZIMS and ZTL. Two species, Pachypanchax varatraza and Paretroplus nourissati, are not listed in ZIMS. The former species, P. varatraza, is kept at Aquazoo Düsseldorf, Germany only and the latter species, P. nourissati, according to ZTL, at ZSL Whipsnade Zoo in United Kingdom; however, the species is only depicted on a display panel at ZSL Whipsnade Zoo, but not really present, thus in fact not held (C. Fusari, pers. comm.).

In total another 11 breeding groups for two members (Pachypanchax omalonotus, P. sakaramyi) of the family Aplocheilidae appear in ZTL (in Austria [1], Czech Republic [1], Germany [5], United Kingdom [2] and Switzerland [1]), which are not recorded in ZIMS.

For two species (Bedotia geayi, B. madagascariensis) of the family Bedotiidae another 12 husbandries appear in ZTL (in Czech Republic [1], Denmark [1], France [1], Germany [4], United Kingdom [1], Hungary [1], Luxemburg [1], Poland [1] and Spain [1]), which are not recorded in ZIMS.

And for seven species (Paratilapia polleni, Paretroplus damii, P. kieneri, P. maculatus, P. menarambo, Ptychochromis grandidieri and P. insolitus) of the family Cichlidae another 29 husbandries appear in ZTL (in Austria [1], Germany [2], United Kingdom [5], France [2], Netherlands [1], Poland [1], Russia [4], Spain [1]), which are not recorded in ZIMS (Paretroplus nourissati was excluded here for the reasons given above).
5.1 | Threatened endemic Malagasy freshwater fish species that are not yet held in captivity

In total 31 endemic, threatened (IUCN, 2020) Malagasy freshwater fish species are not yet held in zoos globally according to ZIMS (Table 6).

5.2 | Threatened Malagasy freshwater fish species kept by hobbyists

Two private owners from the Facebook group “Madagascar Endangered Fishes” have responded to our survey released in June 2020. Accordingly, at least 15 endemic Malagasy freshwater fish...
FIGURE 6  Continued
TABLE 5 Total number of Malagasy freshwater fishes that successfully reproduced in zoos during the 12 months preceding our survey (ZIMS)

| Family       | Species                  | Institution                  | Offspring | Total |
|--------------|--------------------------|------------------------------|-----------|-------|
| Aplocheilidae| *Pachypanchax amoulti*   | ZSL London Zoo               | 13        | 16    |
|              |                          | Toronto Zoo                  | 3         |       |
|              | *P. omalonotus*          | Wroclaw Zoo                  | 20        | 20    |
|              | *P. sakaramyi*           | ZSL London Zoo               | 16        | 63    |
|              |                          | Leipzig Zoo                  | 20        |       |
|              |                          | Ostrava Zoo                  | 9         |       |
|              |                          | New York Aquarium (Brooklyn) | 18        |       |
| Bedotiidae   | *Bedotia geayi*          | Wroclaw Zoo                  | 15        | 73    |
|              |                          | New York Aquarium (Brooklyn) | 8         |       |
|              |                          | Cleveland Metroparks Zoo     | 50        |       |
|              | *B. madagascariensis*    | Zoological Garden Bernburg   | 13        | 129   |
|              |                          | Fota Wildlife Park (Ireland) | 50        |       |
|              |                          | Cologne Zoo                  | 66        |       |
|              | *B. marojeyi*            | Toronto Zoo                  | 6         | 6     |
|              | *Rheocles vatosoa*       | ZSL London Zoo               | 72        | 93    |
|              |                          | Toronto Zoo                  | 21        |       |
| Cichlidae    | *Paretroplus kieneri*    | Leipzig Zoo                  | 25        | 30    |
|              |                          | Bronx Zoo                    | 5         |       |
|              | *Ptychochromis insolitus*| Cologne Zoo                  | 158       | 158   |
|              | *P. loisellei*           | Cologne Zoo                  | 50        | 135   |
|              |                          | Toronto Zoo                  | 85        |       |

species are kept by private breeders (Table 7). Of them, *Ptychochromis grandidieri* is Not Threatened (LC), and *P. mainty* Data Deficient (DD). Three of the privately kept species are not yet represented in zoos according to ZIMS and ZTL: the aplocheilid *Pachypanchax sparksorum* and the cichlid species *Paretroplus dambabe* and *P. nourissati*.

5.3 | Discussion and recommendations

Of the 173 freshwater fish species from Madagascar, 123 are exclusively found in pure freshwater. Of these, 97 species are native, and 79 are endemic to Madagascar (see Table 1). In the past two

TABLE 6 Threatened endemic Malagasy freshwater fish species that are not yet held in captivity (ZIMS), including ZTL information (n = 31); sorted alphabetically by family including conservation status (IUCN, 2020) and information on micro-endemism (xx)/regional endemism (x)

| Family       | Species                  | Status  | Endemism |
|--------------|--------------------------|---------|----------|
| Anchariidae  | *Ancharius griseus*      | EN      |          |
|              | *Gogo ornatus*           | EN      |          |
| Aplocheilidae| *Pachypanchax sparksorum*| EN      |          |
| Ariidae      | *Arius festinus*         | CR      | xx       |
|              | *Arius uncinatus*        | CR      | xx       |
| Atherinidae  | *Teramulus waterloti*    | EN      |          |
| Bedotiidae   | *Bedotia albomarginata*  | EN      |          |
|              | *B. leucopteran*         | EN      |          |
|              | *B. masoala*             | VU      | xx       |
|              | *B. tricolor*            | CR      |          |
|              | *Rheocles alaotrensis*   | EN      |          |
|              | *R. derhami*             | CR      | xx       |
|              | *R. lateralis*           | CR      |          |
|              | *R. wrightae*            | EN      |          |
| Cichlidae    | *Katria katria*          | EN      | xx       |
|              | *Oxylapia polli*         | EN      | xx       |
|              | *Paretroplus. dambabe*   | CR      |          |
|              | *P. gymnoperipercularis* | CR      |          |
|              | *P. lamenabe*            | EN      |          |
|              | *P. maromandia*          | EN      |          |
|              | *P. nourissati*          | EN      | x        |
|              | *P. tsiomy*              | EN      |          |
|              | *Ptychochromis inornatus*| EN      |          |
|              | *Ptychochromoides betsileanus* | CR |          |
|              | *P. itasy*               | CR      | xx       |
|              | *P. vondrozo*            | EN      |          |
| Clupeidae    | *Sauvagella robusta*     | EN      |          |
| Kuhliidae    | *Kuhlia sauavagii*       | VU      |          |
decades, more than 20 freshwater fish species have been scientifically named from Madagascar (see overview in Ziegler et al., 2020), which on average is at least one new species named each year. It can be assumed that even in the well-studied groups (cichlids, aplocheilids, bedotiids) further species will be discovered in the future, in particular micro-endemic taxa prone to extinction. Furthermore, the taxonomy of several rather species-rich families such as the Eleotridae and Gobiidae have not been thoroughly revised in Madagascar using integrative approaches, i.e., including molecular data sets, and it is likely that numerous unnamed species exist in these groups.

Besides the need for further field research in Madagascar in concert with intensified taxonomic revisions, the conservation status of many taxa also needs re-evaluation. Such re-assessment is needed for numerous Malagasy freshwater fish species whose threat situation has worsened locally since the last evaluation (Ziegler et al., 2020). For a number of species, assessments are so far completely lacking, such as for the micro-endemic anchariids Gogo arcuatus and Gogo brevibarbis. Also the cichlid Ptychochromis makira is classified DD due to the lack of a comprehensive survey. For 17 of the 79 known endemic Malagasy freshwater fish species, an assessment has so far not been possible due to insufficient data (DD) or lack of research (NE). With new assessments, the percentage of threatened endemic Malagasy freshwater fish species (63%) will certainly increase substantially. First recommendations were made by Ziegler et al. (2020), who suggested to upgrade Gogo atratus and Ptychochromis ernstmagnusi from DD to VU, and Ptychochromis sakaramyi from EN to CR. Even the number of species classified as Extinct by the IUCN (2020) (Ptychochromis onilahy and Pantanodon madagascariensis) could be underestimated (Máíz-Tomé et al. 2018). There might also be a few taxa to be downranked in threat status, such as Bedotia leucopteran, B. madagascariensis, Ptychochromis patriciae, Ptychochromis oligacanthus, and Sauvagella robusta (Ziegler et al., 2020).

According to our analysis of ZIMS data, 20 Malagasy freshwater fish species are kept in zoos worldwide, with 18 of them being endemic and threatened. By adding information from the Zootierliste database we could add the Endangered Pachypanchax varatraza (in Aquazoo Düsseldorf) which was not included in the ZIMS data, but which since recently also is held at the Cologne Zoo. This number of 19 endemic, threatened Malagasy freshwater fish species held amounts for less than one fourth only of the 79 endemic Malagasy freshwater fish currently recognized. Our assessment is probably not complete, however, given that ZIMS is used by around 1100 institutions worldwide (Species360, 2020), we are convinced the numbers presented here are quite representative of the actual situation. Hence, it is likely that more than half of the 50 threatened endemic Malagasy freshwater fish species (viz. 31 species) have no ex situ conservation component (see Table 6).

The paramount importance of ex situ conservation for Madagascar's freshwater fishes has been stressed by Benstead et al., (2003). Given that the combination of deforestation, overfishing, and exotic species introduction has affected most of Madagascar's freshwater habitats, captive breeding represents the only guaranteed means of saving a large proportion of Madagascar's endemic fishes from extinction—although persistence within original habitat continues being the optimal conservation strategy (Benstead et al.,

| FAMILY | SPECIES | STATUS | ENDEMISM |
|--------|---------|--------|----------|
| Milyeringidae | Typhleotris madagascariensis | EN | x |
| | T. mararybe | CR | x |
| | T. pauliani | CR | x |

Abbreviations: CR, critically endangered; EN, endangered; VU, vulnerable.
Eighteen years ago, captive breeding efforts undertaken by public aquariums, zoos, and individuals in North America and Europe had resulted in the establishment of managed populations of 32 Malagasy fish species (Benstead et al., 2003).

However, with currently 19 threatened endemic Malagasy freshwater fishes held in zoos according to our analysis, the situation has not much improved since the strong beginning in the early 2000s. If we add the species confirmed through our survey held by private keepers (Pachypanchax sparkorum, Paretroplus dambabe, P. nourissati), there is evidence for a total of 22 threatened endemic Malagasy freshwater fishes currently held ex situ—most of them in Europe and the USA, and some of them at single or few institutions only. In total, eleven endemic species are classified as Critically Endangered, thus facing an extremely high risk of extinction in the wild, but which are not yet kept ex situ (Table 8). To obtain a stable conservation breeding network, we strongly recommend increased efforts to better distribute species among institutions, to prevent the loss of a given species due to unforeseen local events such as disease outbreak, accidents, natural disasters or technical failures (see also Jacken et al., 2020; Wahle et al., 2021).

A first initiative to move in this direction was the kind provision in 2019 of Ptychochromis insolitus, P. loisellei and Rheocles vatoosa offspring from Toronto Zoo in Canada to Cologne Zoo in Germany to enable the keeping of and the breeding of these species in Europe. Of these species, P. loisellei was previously not present in any European zoo, and P. insolitus had previously been only kept in London Zoo in the United Kingdom (from 2002 to 2014) and for some time in the past in Berlin Zoo in Germany, without reproduction. Since the transfer, several hundreds of fry of the two Ptychochromis species have already been produced in Cologne Zoo, and more than 300 offspring of both species have been transferred to more than ten zoos in Germany and Europe, with hundreds of further juveniles available for further distribution (Ziegler et al., 2020). Rheocles vatoosa also reproduced meanwhile at the Cologne Zoo.

We recommend to expand the recently seeded conservation breeding network for these cichlids (not yet reflected in the ZIMS data summarized herein) to further species. For instance, our analysis identified several potential transfer opportunities within Europe (Figures 5 and 6), e.g., of Pachypanchax arnoulti that is kept in only two European zoos and has reproduced lately at ZSL London Zoo only, if we add the species confirmed through our survey held by private keepers (Pachypanchax arnoulti). Of these species, P. loisellei is highly represented in European captive holdings, and keeping instead one of the threatened species might be advisable at least in some cases. Recommendations are given in Table 8. However, circumstances can change quickly and should be considered as well. For example, Ptychochromis insolitus was among the rarest fishes only a few years ago. Only through the recent buildup of a conservation breeding network (Ziegler et al., 2020), the species is no longer listed with top priority in Table 8—which it would have had deserved only a few years ago.

Of the 19 threatened endemic Malagasy freshwater fish species kept in zoos worldwide, nine species (with Bedotia geayi in zoos treated as B. madagascariensis) have reproduced recently. Certainly, the success of captive breeding can be improved through better exchange of individuals and information, optimized transfers, and a focus on species that did not yet reproduce. This also should involve private breeders which can be key to a successful conservation breeding program. For instance, the Cologne Zoo received offspring of the rarely kept Ptychochromis oliganthus from a private breeder recently, and they have already begun to reproduce. The aplocheilid Pachypanchax sparkle and the cichlids Paretroplus dambabe and P. nourissati are currently held only by private breeders. Here, zoo-based conservation breeding programs of these threatened species should be established based on private surplus (Table 8).

In turn, zoos can and should get involved in transferring offspring to specialized private breeders and include these in the conservation breeding network. Recently, the initiative Citizen Conservation (CC), which involves dedicated private keepers (www.citizen-conservation.org) has launched a breeding program starting, e.g., with Ptychochromis insolitus and P. loisellei, with plans to include even more threatened Malagasy fishes in the near future. This exemplifies the potential for a powerful synergy between zoos and private holders in ex situ conservation of small-sized vertebrate species. Increasing number of holdings in Table 8 thus also implies CC facilities.

As previously mentioned, field research in Madagascar must continue to uncover overlooked freshwater fish diversity before it is lost. This should also be increasingly tied to conservation breeding efforts, as it is crucial to legally allow the capture and transfer of threatened taxa to set up ex situ populations of species not yet kept in captivity. Ideally, the strategy should include ex situ holdings in Madagascar, such as a domestic freshwater fish breeding facility in Andapa managed by Association des Producteur Privés d’Alevis (APPA). However, distributing insurance populations also among various institutions abroad continue being essential to be better prepared for catastrophic events affecting the local facilities.
TABLE 8  Topical recommendations for improved conservation breeding network for Malagasy freshwater fish species currently listed as threatened by IUCN (2020); Ziegler et al. (2020) recommended *Gogo atratus* and *Ptychochromis ernstmagnusi* to be upgraded from DD to VU, and then they would have to be added to the list under the category “establish ex situ population” with xxx and x; as DD species *Gogo brevibarbis* and *Ptychochromis makira* are not included, but as micro-endemic species ex situ populations should likewise be established for; them according to Ziegler et al. (2020), *Sauvagella robusta* may move from EN to LC.

| Threatened endemics (IUCN status) | Establish ex situ population | Increase number of holdings | Transfer surplus from hobbyist to zoo | Husbandry |
|-----------------------------------|-----------------------------|-----------------------------|--------------------------------------|------------|
| **Anchariidae**                   |                             |                             |                                      |            |
| Ancharius griseus (EN)            | xx                          |                             |                                      |            |
| Gogo ornatus (EN)                 | xx                          |                             |                                      |            |
| **Apocheilidae**                  |                             |                             |                                      |            |
| *Pachypanchax amoutli* (VU)        |                             | xxx                         | Zoo expertise                        |            |
| *P. omalonotus* (EN)              |                             | xx                          | Sterba (1990), Mailliet (2006),      |            |
|                                   |                             |                             | private and zoo expertise            |            |
| *P. patriciae* (EN)               |                             | xxx                         | zoo expertise                        |            |
| *P. sakaramyi* (EN)               |                             | x                           | Schäfer (2018), Ziegler et al. (2020),|            |
|                                   |                             |                             | private and zoo expertise            |            |
| *P. sparksorum* (EN)              |                             | xxx                         | Private expertise                    |            |
| *P. varatraza* (EN)               |                             | xxx                         | Private and zoo expertise            |            |
| **Ariidae**                       |                             |                             |                                      |            |
| Arius festinus (CR)               |                             | xxx                         |                                      |            |
| A. uncinatus (CR)\*End            |                             | xxx                         |                                      |            |
| **Atherinidae**                   |                             |                             |                                      |            |
| Teramulus waterloti (EN)          |                             | xx                          |                                      |            |
| **Bedotidae**                     |                             |                             |                                      |            |
| Bedotia albomarginata (EN)        |                             | xx                          |                                      |            |
| *B. geayi* (EN)\*End              |                             | xxx                         |                                      |            |
| *B. leucopteran* (EN)\*End        |                             | xx                          |                                      |            |
| *B. longionalis* (EN)             |                             | xxx                         | Mailliet (2004), zoo expertise       |            |
| *B. madagascariensis* (EN)\*stable|                             |                             | Mailliet (2004), private and zoo    |            |
|                                   |                             |                             | expertise                            |            |
| *B. marojejy* (EN)                |                             | xxx                         | Mailliet (2004), zoo expertise       |            |
| *B. masoala* (VU)\*End            |                             | xxx                         |                                      |            |
| *B. tricolor* (CR)                |                             | xxx                         |                                      |            |
| Rheocles alootrensis (EN)         |                             | xx                          |                                      |            |
| *R. derhami* (CR)\*End            |                             | xxx                         |                                      |            |
| *R. lateralis* (CR)\*End          |                             | xxx                         |                                      |            |
| *R. vatosoa* (EN)\*End            |                             | xxx                         |                                      |            |
| *R. wrightae* (EN)                |                             | xx                          |                                      |            |
| **Cichlidae**                     |                             |                             |                                      |            |
| Katria katria (EN)                |                             | xx                          |                                      |            |
| Oxylapia polli (EN)\*End          |                             | xxx                         |                                      |            |

(Continues)
Together such a strategy complies with the One Plan Approach proposed by the IUCN SSC Conservation Breeding Specialist Group (CBSG), viz. the development of management strategies and conservation actions by all responsible parties for all populations of a species, whether inside or outside their natural range. As exemplified by the multidisciplinary approach by Fish Net Madagascar (https://fishnetmadagascar.com/), any strategy must consider that in the long term ex situ measures can only prove successful in concert with a perspective for in situ conservation actions to restore and long-term protect a species' natural habitat.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

The protocol and procedures employed were ethically reviewed and approved by Cologne Zoo’s director and the Madagascar Fauna and Flora Group.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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