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Species depauperate communities and low abundances of monogenean gill parasites at the edge of the natural distribution range of their cichlid hosts in northern Africa

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Abstract

In Morocco, no work has been carried out on parasitic monogeneans of cichlid fish. An examination of the gills of 375 fish from three native species of Cichlidae: *Oreochromis aureus, Coptodon zillii* and *Coptodon guineensis* from different localities, revealed the presence of two monogenean species (1328 monogenean specimens were recovered from 56 fish specimens) belonging to the family Dactylogyridae and to the genus *Cichlidogyrus*: three morphotypes of *C. cirratus* were identified from *O. aureus* and *C. zillii*; and *C. cubitus* was identified from *C. guineensis*. This is the first time that these monogeneans were collected and identified in Morocco. In addition, *O. aureus* was revealed as a new host for *C. cirratus*. The low parasite species richness and intensity, appear to support the enemy release hypothesis, and have probably promoted the lateral transfer of parasites in natural populations between *O. aureus* and *C. zillii*, and the synxenic diversification of *C. cirratus*.

Keywords: Morocco, enemy release hypothesis, lateral transfer, morphotypes, synxenic diversification.

Introduction

The diversification of continental aquatic organisms is the result of different events linked on the one hand to the evolutionary potential of the species, and on the other hand to the duration of hydrographic isolations, to the size of the watersheds and also to the diversity of aquatic habitats. Currently, ichthyologists distinguish the existence of several large main ichthyological provinces in Africa; Morocco being between the Maghreb province and a Saharan zone (Lévêque et al., 1997).

These two zones, located between the African and European tectonic plates, are characterized by a very poor fish fauna, of which Cyprinidae Rafinesque, 1815 is the most widespread family. In the Maghreb province cyprinid fishes have the highest species diversity (70.7%) (Doadrio, 1994), with 20 valid species in Morocco alone (Rahmouni, 2020).

Another family, with a mostly tropical distribution, is also present: Cichlidae Heckel, 1840 (Doadrio, 1994; Lévêque & Paugy, 2006). This family represents one of the most species-rich fish, with conservative estimates citing about 3000 extant species on earth (Takahashi & Koblmüller, 2011). Cichlids are widely distributed in Africa, Central and South America, the Middle East and parts of South Asia, while fossils have been found in Europe (Italy) (Nelson, 1994). In Morocco, cichlids are tropical relics from the last glacial episodes (Lévêque, 1990); they are represented by small isolated populations (Louizi et al., 2019). They are naturally represented by only two genera: *Coptodon* Gervais, 1848 and *Oreochromis* Günther, 1889, with three native species: *Coptodon zillii* (Gervais, 1848), *C. guineensis* (Günther, 1862), and *Oreochromis aureus* (Steindachner, 1864). A fourth species, *O. niloticus* (L, 1758), has been introduced into northern Morocco for aquaculture purposes (Louizi et al., 2019; Ainou et al., 2021).

To date, African cichlid fishes are known to be parasitized by members of six genera of monogenean parasites (Platyhelminthes): the representatives of two of them are mesoparasites (*sensu* Euzet, 1989) living in a natural cavity of the host (*Enterogyrus* Paperna, 1963 in the stomach; *Urogyrus* Bilong Bilong, Birgi and Euzet, 1994 in the urinary bladder) and four are ectoparasites (Pariselle et al., 2011). The members of three of these are found on the gills and belong to Dactylogyridae: *Cichlidogyrus* Paperna, 1960, *Onchobdella* Paperna, 1968 and *Scutogyrus* Pariselle & Euzet, 1995 (Pariselle et al., 2011) while one genus, mainly found on the skin and on the fins, belongs to Gyrodactylidae: *Gyrodactylus* von Nordmann, 1832. Among these, *Cichlidogyrus* is the most species-rich, including 138 described species in Africa and Middle East (Cruz-Laufer et al., 2021).

Contemporary ecology has widely emphasized the importance of parasites as models for studying the structure and organization of communities (Kmentová et al., 2020). Their assessment represents a simple and inexpensive way of collecting ecological information about their hosts (Williams et al., 1992; Poulin, 2021). Monogeneans present an often high level of host specificity; several studies showed that this specificity may reflect the evolution, phylogeny, historical biogeography and ecology of host species (Pariselle et al., 2003; Vanhove et al., 2016; Pariselle et al., 2011; Boeger et al., 2003; Cruz-Laufer et al., 2022).

Parasite species richness varies according to several host- or parasite-dependent factors such as the maximum size (Guégan et al., 1992) and the ethology of the host, the environment in which the host species lives, the geographical distribution of the host (Combes, 2001), the number of parasite species inherited from the ancestral host species, lateral transfers or host switches, evolutionary changes of the host specificity of a parasite that can occur between related host species (Pariselle et al., 2011) or even between phylogenetically distant host species, in natural or artificial conditions (Vanhove & Huyse, 2015), stochastic losses of parasitic species (following bottleneck events experienced by host populations) (Pariselle et al., 2003), etc.

The survival of introduced host populations may be favored by the loss of their original parasitic fauna (lower parasitic species richness and relatively lower parasite load) following the enemy release hypothesis (ERH) (Mlynarek et al., 2017). This theory assumes that introduced host species gain permanent or temporary advantage compared to the local fauna by losing their native parasites (Torchin et al., 2003). Introduction of alien populations may also result in three possible effects (Sheath et al., 2015): spillback "occurs when parasites from native hosts transfer to the introduced alien host and there is increase in infection", dilution "occurs when there is a decrease in the infection of the native hosts as aliens reduce transmission of parasites", and spillover "might occur when an alien host introduces new parasites which then parasitise novel hosts in the new range" (Truter et al., 2017).

In Morocco, cichlid fishes are in the northern limit of their natural distribution area, where they arrived a long time ago from sub-Saharan areas. During this long-distance dispersal process, they probably experienced many bottleneck events, as was the case for present-day anthropogenically introduced populations. The fact that Moroccan cichlid fishes now survive in suboptimal conditions may have been enabled by the enemy release hypothesis. For example the low lethal temperature for *O. aureus* ranges from 8 to 15 °C (Rezk & Kamel, 2011), temperature that are common in Moroccan rivers. They also may have been subject to spillback/over effects.

The present study aimed to test these expected scenarios in Morocco on native (non-invasive) species at the edge of the natural distribution range, by studying their gill monogenean fauna diversity using the quantitative descriptors of parasite communities by Bush et al. (1997).

Materials and methods

Fish sampling and identification:

Cichlids, identified following Teugels & Thys van den Audenaerde (1992), were caught in various rivers, gueltas (ponds fed by a source generally corresponding to an oasis), wadis and sebkhas (a type of salted wetland in the hot desert regions of North Africa) of Morocco from 2010 to 2021, by either gillnets (length: 20 m, height: 2 m; extended mesh size: 60 and 80 mm) or electrofishing using a portable Samus 725G Fish Shocker Stunner (adjusted according to the physicochemical descriptors of the water) connected to a 12V battery. A total of 66 sampling points, in all the watersheds of the North, West, East and South of Morocco (Fig. 1) were sampled using gillnets or electrofishing. Specimens were euthanized by severing their spinal cord, and either dissected in the field immediately after fishing following Justine et al. (2012) or stored in a portable deep freezer (Engel) until examination in the lab.

Collection and identification of monogeneans:

For the collection of monogeneans, gill arches were placed in a Petri dish, and thoroughly rinsed using a wash bottle and tap water. Monogeneans observed under a stereomicroscope (Leica ES2) were removed using an entomological needle mounted on a mandrel, and placed between slide and coverslip in Malmberg's medium (glycerin ammonium picrate) (Malmberg, 1957). After 24 hours, the slide was sealed with Glyceel (Bates, 1977). The mounts were then observed under a microscope (Leica DM500) and the identification of the monogeneans followed the identification key of Pariselle & Euzet (2009).

Ecological analysis:

In this study, we use the quantitative descriptors of parasites proposed by Bush et al. (1997):

- Prevalence (P%).
- Mean Intensity (MI).
- Parasitic abundance (A).

Parasites were classified as dominant if (P > 50%), satellite if (10 ≤ P ≤ 50%) or rare if (P < 10%) according to Valtonen et al. (1997). For the Mean Intensity (MI), they were classified according to Bilong Bilong & Njiné (1998), namely: MI> 100 (high); 50 <MI ≤ 100 (average); 10 <MI ≤50 (low); MI <10 (very low).

Statistical analysis:

The Chi square (x^2) test was used to compare the Prevalences. The one-way ANOVA was used to compare the Abundances and Mean Intensities of the different localities. The differences were considered significant at the 5% level. These tests were performed using STATISTICA 10.0 software.

Results

A total of 375 fish specimens were collected and identified as *Coptodon zillii* [n = 80, TL = 10.87 ± 1.56 (7.5–14.7)], C. *guineensis* [n = 240, TL = 14.27 ± 3.79 (8.2–23)] and *Oreochromis aureus* [n = 55, TL= 16.55 ± 3.15 (9.8–22.5)]. *Coptodon zillii* and *O. aureus* were found in the Draa basin in sympatry (W. Draa, Mrimima and G. Zerga), except for localities W. El Maleh where only *C. zillii* and G. Kehla where only *O. aureus* were sampled. *Coptodon guineensis* was found in the Canal de Nador (W. Drader), Chebika Basin (W. Chebika and W. Aabar), and in the Sebkha Imlili (Fig. 1, Table 1).

A total of 1328 monogenean specimens were recovered: *Cichlidogyrus cubitus* Dossou, 1982 (n = 149) from *C. guineensis*, and three morphotypes of *C. cirratus* Paperna, 1964 (here referred under the working names *C. cirratus* s.s., *C.* "cirratus 1" and *C.* "cirratus 2") from both *O. aureus* (n = 1150), and *C. zillii* (n = 29). The morphotypes were identified (Fig. 2 A) by their male copulatory organ (MCO).

Cichlidogyrus "cirratus 1" (Fig. 2 B) differs from *C. cirratus* s.s. (Fig. 2 A) by the shape of the extremity of the accessory piece: two smooth and rounded ends of almost equal size vs one end hook-shaped, respectively. This particular morphology of the accessory piece is found only in *C. mbirizei* Muterezi (Bukinga et al., 2012) described from *Oreochromis tanganicae* (Günther, 1894) in Lake Tanganyika (East Africa). *Cichlidogyrus mbirizei* is distinguished by a spirally coiled vagina while it is sinuous in *C.* "cirratus 1" (and *C. cirratus* s.s. and *C.* "cirratus 2").

The morphotype *C.* "cirratus 2" (Fig. 2 C) is very similar to *C.* "cirratus 1" with regard to the morphology of its haptor, MCO and vagina. Nevertheless, it differs by the shape of the accessory piece termination which presents two ends, one is a short rounded outgrowth and the other, longer, has a hook-shape vs two rounded ends in *C.* "cirratus 2" (and one hook-shaped in *C. cirratus s.s.*) and by the direction of the heel which rises posteriorly in *C. mbirizei* (and *C. cirratus s.s.*) and anteriorly in *C.* "cirratus 2" (and *C.* "cirratus 1").

Cichlidogyrus cubitus (Fig. 2 D) has a thin open C-shaped MCO with a developed basal ampulla. The sharply angled accessory piece is attached to the basal ampulla of the MCO, the end is bifid, one of the points is twice as long as the other, and the heel is reduced.

The values of the quantitative descriptors of parasite from *O. aureus*, *C. zillii* and *C. guineensis* are presented in Table 2, which shows that the infection parameters of *C. cirratus* (3 morphs) and *C. cubitus* varied between localities.

Morphotypes of *C. cirratus* were present on all the sampled populations of *O. aureus* (W. Draa (P = 100%), Mrimima (P = 77.8%) and G. Zerga (P = 57.1%)), except locality G. Kehla. All the morphotypes were found on one specimen of *C. zillii* in locality W. Draa (P = 6.67%), whereas this host carried only *C. cirratus s.s.* in locality Mrimima (P = 3.1%). Monogeneans were absent on this host in localities W. El Maleh and G. Zerga. In contrast, *C. cubitus* was only present on *C. guineensis* at locality W. Aabar (P = 32.8%).

The three morphotypes of *C. cirratus* were dominant species (P> 50%) on localities W. Draa (*O. aureus* and *C. zillii*), Mrimima and G. Zerga (*O. aureus* only). *Cichlidogyrus cirratus s.s.* was rare in locality Mrimima on *C. zillii*. *Cichlidogyrus cubitus* was a satellite species on *C. guineensis* in locality W. Aabar. Finally, the mean intensity for all parasites (the 3 morphs of *C. cirratus* and *C. cubitus*) varies from low (10 <MI ≤50) to very low (<10) among the localities.

The Chi square statistical test carried out on the prevalences according to the hosts (*O. aureus* and *C. zillii*) (x^2 = 3.79, df = 2, p = 0.14) and the ANOVA on the mean intensities and the abundances (F = 0.53, dl = 2, p = 0.59) showed no significant difference between the localities.

Discussion

North Africa, and in particular Morocco, is part of the Palearctic and more particularly of the Mediterranean biogeographical region. The cichlid species naturally present in Morocco are relict populations of the tropical fauna present during the last glacial episodes when the Sahara was a humid region (Paugy et al., 2011); (Ballouche, 2017). The Sahara acts as a barrier to dispersal between the Palearctic and the Afro-tropics. This is why freshwater fish species of Afrotropical origin are poorly represented in North Africa and we therefore encounter a fauna that is mainly of European origin, dominated by the cyprinid species (Doadrio, 1994).

The North of the Sahara receives little water and currently only has a few residual permanent aquatic environments: the gueltas, some lakes and some sebkhas. The three species of Cichlidae, present naturally in Morocco, have different ecological requirements. While *C. zillii* and *O. aureus* generally live in the middle course of rivers, *C. guineensis* is found more in estuaries or brackish lagoons (Lévêque et al., 1992). The presence of *C. zillii* and *O. aureus* living in sympatry in the lower valley of the Draa watershed is therefore not surprising. The likely absence of *C. guineensis* at the mouth of this Wadi could be due either to a too northern position [which is unlikely since *C. guineensis* has recently been recorded from the Canal de Nador (Ainou et al., 2021)], or to a disappearance of this species over the time as the mouth of the Wadi Draa is very small, often dries up and is subject to substantial seasonal floods. The absence of these same two species (*C. zillii* and *O. aureus*) in the Al Wa'er, Oumma Fatma and Chbika wadies complex could have an opposite explanation: either they never reached this wadies complex over the course of time in view of its isolation, or they disappeared following episodes of drought. On the other hand, *C. guineensis*, the only one present in this watershed, was able, after having arrived from the sea, to move upstream in these wadies in the absence of competition with *C. zillii* and therefore colonize these rivers upstream of their mouth (Louizi et al., 2019). Recently, two specimens of *C. guineensis* were unexpectedly found in the Canal de Nador (Ainou et al., 2021), nearly 1000 km north of the Wadi Aabar, the northernmost locality where this species was previously recorded (Qninba et al., 2012). Probably, this species could have colonized the Canal de Nador via the sea (an ancient (Holocene) or contemporary colonization Ainou et al. (2021)). Cichlid fish are now living at the northern limit of their distribution area, where the populations tend to be more constrained by abiotic factors, to be smaller and more genetically isolated (Sexton et al., 2009). Consequently, their diversity in these watersheds is then logically low (Louizi et al., 2019); (Ainou et al.,2021).

Ectoparasitic organisms are at least as sensitive as their hosts to heterogeneous environmental conditions (Wiens, 1989), which may contribute to reducing their species richness (Pariselle et al., 2003). Moreover, they also undergo the bottleneck events experienced by their hosts, on which they are typically overdispersed (Vanhove et al., 2016). Then, it is not surprising that the inventory of branchial monogeneans of cichlids showed a low parasite diversity in Morocco, with only two species (three morphotypes of *C. cirratus*, and *C. cubitus*) recorded, while in West Africa (from where these fish species originate) 17 species of *Cichlidogyrus* were described on *C. guineensis*, 10 on *C. zillii* and 4 on *O. aureus* (Pariselle, 2003). Over the 375 fish examined, only 56 were parasitized from 4 localities.

Cichlidogyrus cirratus was described by Paperna in 1964 on a single specimen from *Sarotherodon galilaeus* (L., 1758) (syn. *Tilapia galilaea*), and was later reported mainly on *O. niloticus*. It was also described under the name *C. nematocirrus* Paperna, 1969 (synonymized with *C. cirratus* by Pariselle & Euzet (2009)) on *O. niloticus* in Lake Volta (Ghana). Our new record of this species on *O. aureus* is not surprising as *O. niloticus* and *O. aureus* are closely related species. Mitochondrial DNA of *O. niloticus* was naturally introgressed by that of *O. aureus* in West Africa (Rognon & Guyomard, 2003); there are natural hybrids of these two species in the wild (Bakhoum et al., 2009). Nonetheless, it is a new record for *C. cirratus* on *O. aureus*, and also its northernmost locality. *Oreochromis niloticus* and *O. aureus* are known to share their parasites belonging to *Cichlidogyrus* (except now *C. rognoni* Pariselle, Bilong Bilong & Euzet, 2003 found only on *O. niloticus*) (see Pariselle & Euzet, 2009).

Although *C. cirratus* had been recorded from *C. zillii* in Lake Albert (Uganda) by Paperna (1979) (with no mention of infection parameters, so likely only few specimens were recovered, potentially indicating accidental infection), it has never been recovered from this host species in Western Africa (Pariselle & Euzet, 2009) despite a great number of hosts examined (Pariselle, 2003). Therefore, the presence in Morocco of *C. cirratus* on *C. zillii* is most probably the result of a lateral transfer (spill over or spill back, see above) between these two distant host species, made easier by the absence of the original species of *Cichlidogyrus* harbored by *C. zillii* [i.e. *C. aegypticus* Ergens, 1981; *C. anthemocolpos* Dossou, 1982; *C. arthracanthus* Paperna, 1960; *C. cubitus* Dossou, 1982; *C. digitatus* Dossou, 1982; *C. ergensi* Dossou, 1982; *C. ornatus* Pariselle & Euzet, 1996; *C. tiberianus* Paperna, 1960; C. *vexus* Pariselle & Euzet, 1995; *C. yanni* Pariselle & Euzet, 1996 (Pariselle, 2003)]. As Gobbin et al. (2021) report that relationships between the number of species of *Cichlidogyrus* were negatively correlated with their abundance, the absence of original monogenean species may considerably reduce interspecific competition and favor colonization by spillover or spillback. Another factor that may also favor this spillover/back effect, is the low density of potential host individuals, which may encourage oncomiracidia (monogenean infectious stages actively infecting a host individual) to infest the first available fish, whether it is the preferred one or not (Pariselle et al., 2015); (Kmentová et al., 2016). The differences in prevalence of *C. cirratus* between the two host species, every time higher on *O. aureus* than on *C. zillii*, is also in favor of the latter not being the original host of this monogenean species (Mladineo & Maršić-Lučić, 2007).

The appearance/cohabitation of different morphs of *C. cirratus* on the same host(s) was likely promoted following the vacancy of the niches on the gill biotope of *O. aureus*. The loss of almost all the original species of

Cichlidogyrus contributes to the potential isolation of several populations of *C. cirratus* followed by synxenic drifts (equivalent to sympatric speciation for parasite species) (Euzet & Combes, 1980). Finally, it is not surprising that the only morphological differences between these morphotypes are visible in the copulatory organs, in fact: the morphology of the genitalia seems to be more useful than the haptoral morphology for species-level identifications, presumably because of its faster rate of change (Pouyaud et al., 2006).In Morocco, *C. cubitus*, which parasitizes *Coptodon* spp. in different locations in West Africa (e.g. *C. dageti* Thys van den Audenaerde 1971; *C. guineensis*; *C. louka* Thys van den Audenaerde, 1969; *C. zillii*) (Pariselle, 2003), is only found on *C. guineensis* in Wadi Aabar. Its absence on Moroccan *C. zillii* is also probably due to a local extinction following bottleneck events suffered by the host populations, which also tend to reduce the parasite species richness (see above and (Pariselle et al., 2003)); or to weak sampling effort. This species is also not found in the Sebkha Imlili where the salinity of the environment (from 39 to 45 g/L) (Agnèse et al., 2018) is probably too high to allow its survival, salt being a common treatment against monogeneans (Schelkle et al., 2011). Following the same spillback/over scenario that we have just sketched for *C. cirratus*, *C. cubitus* was also found in Tunisia on *Haplochromis desfontainii* Lacepède, 1802 (pers. comm. Pr. Lassad Neifar) and it was recorded in Algeria on *C. zillii*, a natural host (Attir et al., 2017).

Conclusion

Generally, the overall ecological conditions become increasingly difficult and stressful as one moves to the edge of the native range of a species (Gaston, 2003). In Morocco, the studied host species and their parasites are therefore at the limit of their distribution area; they are subject to bottleneck events and are isolated in small gueltas, where abiotic conditions are suboptimal (hydrological stress: strong variations in temperature, salinity and oxygen content) (Louizi et al., 2019). The low parasite diversity and load reported herein thus supports the enemy release hypothesis (Drake, 2003). As monogeneans are often specific to their host species, they are relatively unlikely to change hosts via lateral transfer, so the presence of *C. cirratus* on the gills of two sympatric non-congeneric host species reveals a "host-switching" in natural conditions (spillover or spillback), and the coexistence of 3 morphs shows a likely synxenic speciation in process.

Data Availability: The datasets supporting the discussion and conclusions of this article are included within the current study and its figures and tables.

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

Authors' contributions: HL, IR and AP designed and supervised this study. MPMV, MV, OBR, AB contributed to sampling, the collection and identification of fish, and provided scientific background information on the fish. HL, IR, MPMV and AP analysed the data and wrote the paper. All authors critically read and edited the manuscript.

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Figure captions

Figure 1 Map of Morocco indicating the sampling sites, the presence/absence of indigenous cichlid species, and cichlid populations infected by monogeneans. A.O.F & C. Wadies Complex: Al Wa'er, Oumma Fatma & Chbika wadies complex. 1: Canal Nador; 2: Wadi Draa; 3: Wadi El Maleh; 4: Mrimima; 5: Guelta Zerga; 6: Guelta Kehla; 7: Wadi Chebika; 8: Wadi Aabar and 9: Sebkha Imlili.

Figure 2 Opisthaptoral and genital sclerotized parts of *C. cirratus s.s*; (A): *C.* “cirratus 1”; (B): *C.* “cirratus 2” (C) and *C. cubitus* (D). 1: Haptor. *Scale-bars*: 50 μm; 2: Vagina and 3: Male copulatory complex. *Scale-bars*: 10 μm.