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Morphological differentiation in African weakly electric fish (genus Campylomormyrus) relates to substrate preferences

ORIGINAL PAPER

Morphological differentiation in African weakly electric fish (genus *Campylomormyrus*) relates to substrate preferences

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Abstract

Under an ecological speciation scenario, the radiation of African weakly electric fish (genus *Campylomormyrus*) is caused by an adaptation to different food sources, associated with diversification of the electric organ discharge (EOD). This study experimentally investigates a phenotype–environment correlation to further support this scenario. Our behavioural experiments showed that three sympatric *Campylomormyrus* species with significantly divergent snout morphology differentially react to variation in substrate structure. While the short snout species (*C. tamandua*) exhibits preference to sandy substrate, the long snout species (*C. rhynchophorus*) significantly prefers a stone substrate for feeding. A third species with intermediate snout size (*C. compressirostris*) does not exhibit any substrate preference. This preference is matched with the observation that long-snouted specimens probe deeper into the stone substrate, presumably enabling them to reach prey more distant to the substrate surface. These findings suggest that the diverse feeding apparatus in the genus *Campylomormyrus* may have evolved in adaptation to specific microhabitats, i.e., substrate structures where these fish forage. Whether the parallel divergence in EOD is functionally related to this adaptation or solely serves as a prezygotic isolation mechanism remains to be elucidated.

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Introduction

In the absence of allopatric separation, disruptive selection on the feeding apparatus can reduce competition by divergent adaptation with regard to resource acquisition. The famous radiation of Darwin finches is indeed associated with divergent bill evolution (Grant 1999) and serves as a textbook example of *ecological speciation* as barriers to gene flow ultimately evolved between the respective phenotypes (Schluter 2000). Among fish, radiations in cichlids are explained by combined character displacement in the feeding apparatus (i.e. the pharyngeal jaw) and visual cues for species recognition (Sage and Selander 1975).

In the species-rich African weakly electric fish (Mormyridae), a radiation within the genus *Campylomormyrus* gave rise to 15 described species mostly native to the Congo River and its tributaries (Feulner et al. 2007). Although the definite geographic origin of these species remains unclear, most occur in sympatry (Feulner et al. 2009a, b). They exhibit pronounced divergence in the feeding apparatus, i.e. the length, thickness, and curvature of their snout (Feulner et al. 2008; Lamanna et al. 2016), as well as their electric signals (Electric Organ Discharge, EOD) (Tiedemann et al. 2010). While the role of the EOD in electrocommunication [as a prezygotic isolation mechanism (Feulner et al. 2009a, b; Nagel et al. 2018a, b)] and electrolocation [for object location and foraging (von der Emde and Bleckmann 1998; von der Emde 1999)] is well established, the adaptive value of divergent snout morphology has remained enigmatic so far (Feulner et al. 2008). It is further not known, whether the divergence in EOD, beyond its proven function as a prezygotic isolation mechanism, is of adaptive value during feeding as well, under which circumstances EOD would constitute a 'magic trait', triggering both adaptation and reproductive isolation (Feulner et al. 2009a, b).

According to the limited available information, *Campylomormyrus* mostly feeds on insect larvae extracted from the sediment (Marrero and Winemiller 1993; Nwani et al. 2008). It has been suggested that the species-specific shape of the snout may have evolved in response to specific prey or substrate structure (i.e. phenotype–environment correlation) and is coupled with EOD diversification (i.e. EOD characteristics determines prey detected) (Feulner et al. 2007; Feulner et al. 2009a, b). Until now, however, no controlled studies have been performed, neither on the feeding behaviour nor on the stomach content of *Campylomormyrus*, except for *C. tamandua* (Nwani et al. 2008).

The natural habitat of *Campylomormyrus*, i.e. the lower Congo River (a relatively short but hydraulically complex stretch of the river), consists of a series of rapids systems and deep underwater canyons (Jackson et al. 2009; Oberg et al. 2009). These rapids systems and complex hydrology create heterogeneous habitats (microhabitats) on small geographic scales. The microhabitats, along with the hydraulic conditions, have been hypothesized to disrupt fish populations, promoting diversification via natural selection and adaptation (Stewart and Roberts 1976) and—ultimately—speciation (Markert et al. 2010).

Since *Campylomormyrus* species significantly differ in the snout morphology, particularly the length, a snout with certain morphology (e.g. short or long) may have advantages over other snout morphologies when foraging in a certain microhabitat. The trait utility might enable better accessibility to food items and/or more effective suction feeding dynamics.

In this study, we experimentally test the hypothesis that the shape of the snout is related to substrate structure, i.e., species with differently shaped snouts will have different substrate preferences. More specifically, we hypothesize that long-snouted species will prefer stone habitats, as there long snout enables them to reach further into this porous substrate,

while short-snouted species may prefer sandy habitats. Previous ecological and systematic surveys in and near the rapids of the lower Congo River tentatively support this hypothesis, as *C. rhynchophorus* is indeed distributed in the rapids with rocky beds (Stewart and Roberts 1976; confirmed by own observation during 3 field trips; Tiedemann and Kirschbaum unpubl. results), while *C. tamandua* is more frequently encountered upstream the rapids in a more sandy area (Tiedemann and Kirschbaum unpubl. results). Furthermore, stomachs of *C. tamandua* are found to contain sand (Nwani et al. 2008). We tested our hypothesis by experimentally assessing the feeding behaviour in different substrates (sand vs. stones) in three *Campylomormyrus* species with markedly different snout morphologies.

Materials and methods

The three *Campylomormyrus* species used in this study are: the short snouted *C. tamandua* (n = 9), the medium snouted *C. compressirostris* (n = 10) and the long snouted *C. rhynchophorus* (n = 11). All experimental fish were imported from Kinshasa (Democratic Republic of the Congo) or are F1 descendants of imported fish (Nguyen et al. 2017).

Dichotomous choice experiments were performed in a test aquarium (90 × 50 × 50 cm). The tank was fitted with two Plexiglas trays (one at each side) containing either sand (size: 0.2–0.6 mm) or stone gravel (size: 20–150 mm). A plastic tube was placed in the centre between the two trays as shelter. Preliminary experiments were performed to define preference zones, representing a vertical position above the trays (up to 5 cm) where a fish interacted physically with the substrate, see Fig. 1. The preference zone is chosen such that within that zone, the fish is close enough to probe the substrate with its snout (as opposed to just swimming above the substrate).

Prior to the choice test, fish were kept without food for 3 days in a holding tank (to motivate foraging behavior) and subsequently 24 h in the test aquarium (for acclimation). Shortly before testing began, equal amounts of live food were distributed directly onto the two substrates to ensure that the food enters the substrates and is not suspend in the water column. We used only one prey type (Chironomidae larvae). From our rearing experience, we know that this food is equally accepted by all three species. This
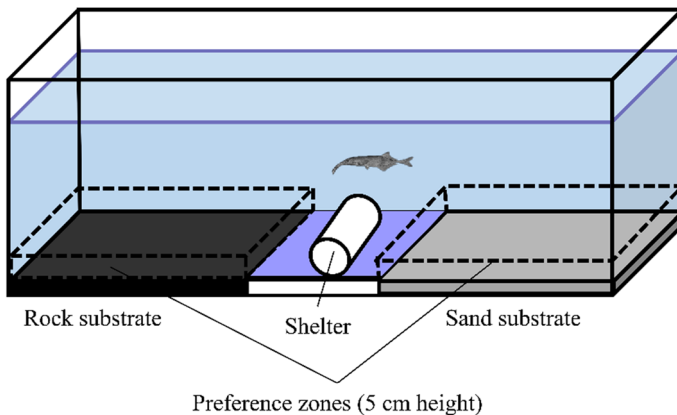

Fig. 1 The experimental tank setup showing the substrates, the shelter, and the preference zones (in dashed lines)

prey was chosen to focus on the effect of substrate structure on the feeding behavior and to minimize potential confounding effects of prey preference. The amount of food was ad libitum, i.e. determined after preliminary experiments such that enough food was available in both substrates throughout the entire experiment.

These three *Campylomormyrus* species are nocturnal, so feeding behaviour was video recorded for 12 h overnight under infrared illumination (30 frames per second, amounting 1,296,000 frames over a 12 h period). To avoid any possible side bias, each fish was tested twice in two different setups of the test aquarium with substrate types switched between sides. We tested all fish first in the first setup, in which the sand substrate is located on the right side and the stone substrate on the left side. The order of fish was selected randomly in this first part of the experiment. After switching the substrates, we tested all the fish again on this 2nd setup, keeping the same order as in the first setup to ensure similar time intervals (25 days) between the two subsequent setups for any specimen.

We developed an algorithm for automated video analysis to determine the exact locations of each fish inside the tank throughout the experiment. The algorithm compares each frame of the video (image) with a background frame (without a fish) by checking the colour of each pixel in the image. Then, it identifies those pixels changed in colour relative to the background (due to the presence of the fish). The algorithm hence detects exactly those pixels capturing the fish at each frame. This algorithm is coded in custom written Matlab routines (R2017a, MathWorks Inc., Natick, MA, USA). For a subset of videos, we validated the code by comparing the locations predicted by the algorithm and the actual locations of the fish and confirmed that the code is accurate in predicting fish locations.

From these data, time spent in the respective preference zones was calculated based on all video frames of the entire experiment duration of 12 h. Fish locations were further processed using a post-processor program (a custom Matlab routine) to calculate the time spent over each substrate and inside the shelter. Using the post-processor program, the position of the fish relative to the preference zones was scored every 2 min to obtain a count number of observations in each preference zone. This post-processing created a reduced data set (from 1,296,000 to 360 frames over a 12 h period) and was applied to minimize tempo-spatial autocorrelation among subsequent data points.

The post-processor program was also used to verify that the time spent over a substrate was associated with foraging and substrate preference. This was achieved by counting probing incidences over each substrate from those video frames retained by the post-processor program, where the fish was in a preference zone. As in previous behavioural studies on *Campylomormyrus* (Feulner et al. 2009a, b; Nagel et al. 2018a, b) and other fish species (Webster and Hart 2004), time spent in the vicinity of a stimulus (here, the substrate) was used as a proxy for preference.

Following Plath et al. (2010), the time data were translated into Strength of Preference (*SOP*) for the stimulus (here, substrate type) to quantify the preference of a fish to a certain substrate. *SOP* was calculated using Eq. 1

$$SOP = (t_1 - t_2)/(t_1 + t_2) \tag{1}$$

where t_1 and t_2 are the total time a fish spent over each substrate.

We used the *SOP* concept in a similar fashion to that of a conspecific versus the heterospecific stimulus. In particular, we assigned the time spent over the sandy substrate to t_1 and that of the stone substrate to t_2 in Eq. 1. Accordingly, *SOP* values could range from -1 (complete avoidance of the sandy substrate and complete preference for the stone substrate)

to 1 (complete preference for the sandy substrate and complete avoidance of the stone substrate). This setting was consistently used for all fish.

A one-sample *t* test was then used to compare *SOP* values against a random distribution of *SOP* = 0. All count data (number of observations, probing incidences, probing incidences per time spent over a substrate) were square-root transformed to yield normally distributed data and then compared using two tailed *t* tests (Sokal and Rohlf 1995).

Results

We first checked the general activity of all fish to ensure that all individuals were fit during the experiment. The activity was monitored by several measures, such as the total swim distance, the swimming velocity, and the ratio of the time spent in/out the shelter for each fish during the experiment. All the fish presented in this study were active during the experiments based on these measures (data not shown).

General activity in all three species indicated a non-random utilization of the aquarium space relative to the position of the gravel trays and the shelter. Fish were close to or inside the preference zones (defined as max. 5 cm distance to the substrate) or the shelter for most of the experiment time (see Fig. 2 for an example). Specimens of the long and medium snouted species, i.e. *C. rhynchophorus* and *C. compressirostris*, spent similar time inside the shelter and foraging, i.e. inside one of the preference zones. However, the short snouted *C. tamandua* spent less time foraging, as compared to time inside the shelter (see Fig. A1 in Additional file 1). There was no significant difference among the species regarding the time spent inside the shelter (one-way ANOVA: $F(2, 27) = 1.97$, $p = 0.158$), while there was a tendency towards such a difference regarding the time spent foraging (one-way ANOVA: $F(2, 27) = 2.69$, $p = 0.085$).

All specimen-specific and experiment-specific results on preference are provided in detail in Additional file 2. These data show that results were consistent across setups (i.e., with sides of the respective substrates switched between left and right). Furthermore, times spent in the shelter and over substrates, respectively, were rather constant throughout entire observation periods (i.e., throughout entire nights; Additional File 3). However, some individuals visited the preference zones, especially the one they prefer, more frequently at the beginning of the experiment, while they visited the shelter more frequently towards the end of the experiment (see Fig. A2 in Additional file 1).

Analysing the time spent in each preference zone showed that *C. rhynchophorus* and *C. tamandua* exhibited a preference for one substrate type (Fig. 2b, c), while *C. compressirostris* did not (Fig. 2a). The long snouted *C. rhynchophorus* showed a significant preference for the stone substrate relative to the sand (SOP = -0.41 ± 0.28 s.d.; one-sample *t* test: $t = 9.922$, $df = 10$, $p < 0.001$; Fig. 3a; see Additional file 2 for individual SOP values). In contrast, the short snouted *C. tamandua* showed a significant preference for the sand relative to the stone substrate (SOP = 0.63 ± 0.20 s.d.: $t = 9.266$, $df = 8$, $p < 0.001$). Only *C. compressirostris*, the species with the intermediate snout size, did not show any consistent preference for a certain substrate (SOP = -0.03 ± 0.21 s.d.: one-sample *t* test $t = 0.495$, $df = 9$, $p = 0.633$). The number of observations of an individual inside a specific preference zone (scored every 2 min) showed a similar pattern (see Fig. A3 in Additional file 1), i.e., *C. rhynchophorus* exhibited a clear preference for the stone substrate (paired-sample *t* test: $t = 4.620$, $df = 10$, $p < 0.001$) and *C. tamandua* showed a strong preference for the sand

Fig. 2 Examples of the fish's location inside the experimental tank over a full 12 h period of observation (heatmap; shifting from blue over yellow to red with increasing time spent at the respective location): **a** no preference to either substrate in a medium snouted *C. compressirostris* specimen; **b** preference of a long snouted *C. rhynchophorus* specimen to the left (stone) over the right (sandy) substrate; and **c** preference of a short snouted *C. tamandua* specimen to the right (sandy) over the left (stone) substrate
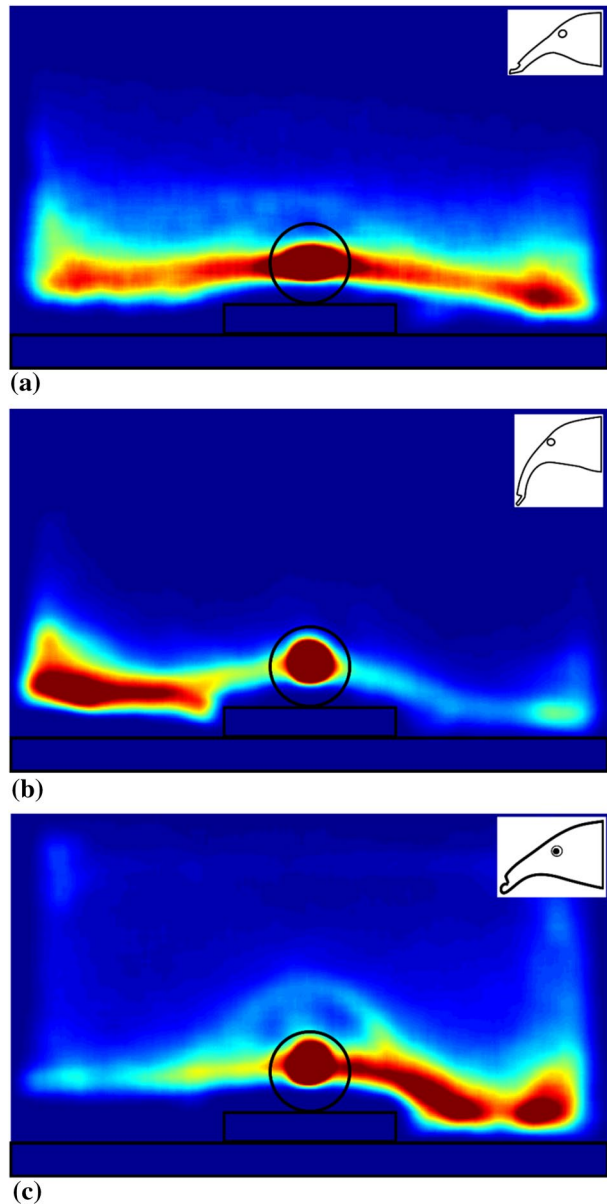
substrate (paired-sample *t* test: $t=9.048$, $df=8$, $p < 0.001$), while *C. compressirostris* had no significant preference (paired-sample *t* test: $t=0.682$, $df=9$, $p=0.511$).

We further verified that presence over a substrate is indeed associated with feeding behaviour: Therefore, we visually scored the probing incidences in each substrate for all individuals (Fig. 3b). In *C. rhynchophorus*, we found significantly more probing incidences over the stone substrate (one-sample *t* test: $t=3.143$, $p=0.010$), while *C. tamandua* individuals showed significantly more probing incidences over the sand substrate (one-sample

Fig. 3 Choice test results for *C. compressirostris* (n = 10), *C. rhynchophorus* (n = 11) and *C. tamandua* (n = 9): **a** association behaviour is displayed as the mean (+ s.d.) time in minutes spent inside the preference zone. **b** Probing incidences counted every 2 min is displayed as the mean (+ s.d.) probing incidences counted inside the preference zone and **c** counted probing incidences per unit time spent over substrates, displayed as the mean (+ s.d)
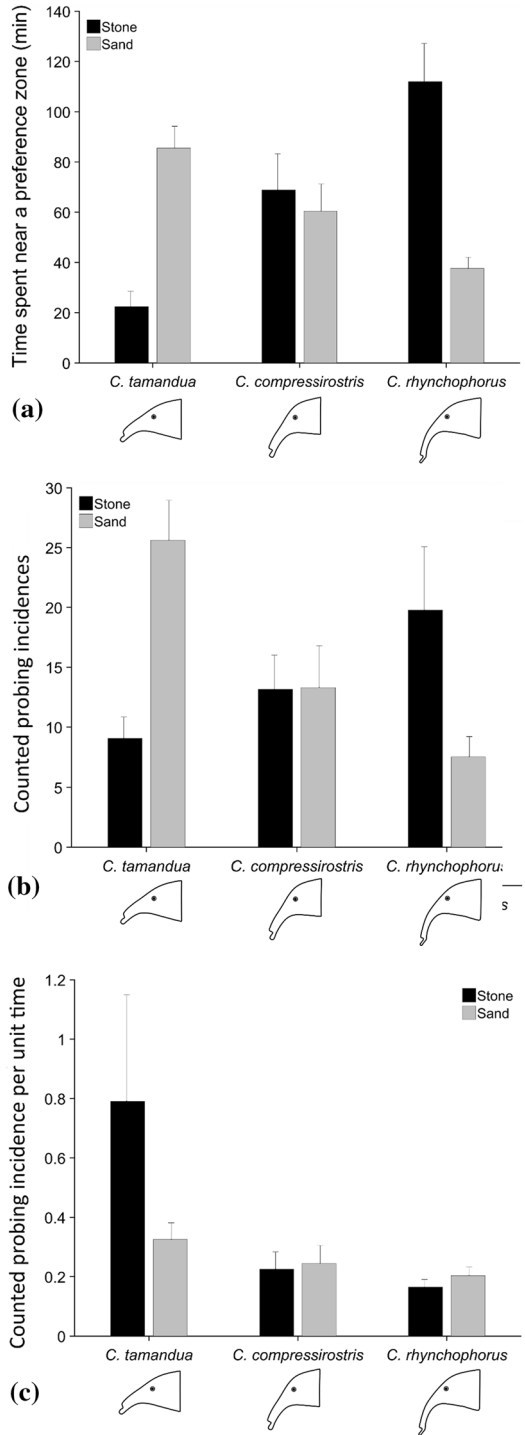
t test: $t = 5.454$, $p < 0.001$). In contrast, the probing incidences of *C. compressirostris* individuals did not vary between the two substrates (one-sample *t* test; $t = 0.033$, $p = 0.974$). This is directly related to the respective time spent over a substrate, as the counted probing incidences (per time unit over a substrate) are similar among species and substrates (*C. compressirostris*: $t = 0.453$, $p = 0.661$; *C. rhynchophorus*: $t = 1.426$, $p = 0.184$; *C. tamandua*: $t = 1.508$, $p = 0.170$, Fig. 3c).

Discussion

Here, we propose that the radiation of African weakly electric fish could be driven in part by snout morphology divergence as an adaptation to foraging on different substrates. We find in three *Campylomormyrus* species, each with different snout morphologies, different preferences for substrate structure while foraging.

Given the phylogeny of the *Campylomormyrus* genus and of the African weakly electric fish in general, short snouts are considered ancestral. In fact, most *Campylomormyrus* species (including the basal *C. tamandua*) and many other mormyrid species (including *Gnathonemus*, the sister taxon of *Campylomormyrus*) display short snouts (Lamanna et al. 2016). Only species of one derived lineage, i.e., *C. rhynchophorus*, *C. numenius*, and *C. curvirostris,* have evolved very long snouts (Feulner et al. 2007; Lamanna et al. 2016).

The medium snout species *C. compressirostris* exploited both substrates without any general preference to a specific substrate structure. Single specimens—however—differed in their *SOP* values (slightly preferring one or the other substrate), but they never exhibited a preference as strong and as consistent across specimens as the preference for stone gravel found in *C. rhynchophorus* or the preference for sand found in *C. tamandua* individuals. *C. compressirostris* may hence represent a more generalist's feeding behaviour with regard to different gravel types encountered in the natural habitat. No information is currently available regarding the natural prey spectrum of *C. compressirostris* and *C. rhynchophorus*, however stomach analyses of the short snout species (*C. tamandua*) confirmed that sand is found in its stomach (Nwani et al. 2008), which agrees well with our findings of a preference for sandy substrate in that species.

The derived long snout species *C. rhynchophorus* significantly preferred the stone substrate over sand, although the individuals used in this experiment were raised in the laboratory and had never experienced natural habitats nor were they trained to distinguish between different substrate structures. The significant preference observed therefore suggests an innate preference for a stony (rather than sandy) substrate. These results support previous studies in weakly electric fish which have highlighted the importance of the snout morphology for foraging (Kristjansson et al. 2002; Schluter and McPhail 1992; Willis et al. 2005). Given their elongated snout, *C. rhynchophorus* may be more capable of foraging in deeper and more complex substrates (i.e., rocky beds). Previous ecological and systematic surveys in the rapids of the lower Congo River also support this hypothesis, as *C. rhynchophorus* is indeed distributed in the rapids with rocky beds (Stewart and Roberts 1976).

A simple mechanistic explanation for the oberved preferences is the observation that long-snouted fish are indeed able to probe deeper into a stony substrate. However, snout length has also implications on suction dynamics. Hence, a mechanistic understanding of the relationship between snout morphology and substrate preference necessitates consideration of suction feeding hydrodynamics to understand the functional implications

of a particular snout type, as well as performance data on snout utility for given prey species and microhabitats.

Our study specifically focussed on the substrate structure as the main factor in the microhabitat and hence offered a prey equally accepted by all three species. However, natural habitats are likely to offer more complex prey spectra. We did not test here, whether snout morphology and/or associated divergence in the electric organ discharge (EOD) are adapted to specific prey spectra. Hence, although preference of stony substrate by a long-snouted species—as found here—is plausible, as this snout is indeed used to probe deep into the substrate, substrate preference may be confounded with availability of a preferred prey type in a particular substrate. Future research on *Campylomormyrus* species in their natural habitat is needed to determine if different snout morphologies translate into different prey spectra.

Regarding EOD divergence, the major role of electrolocation in prey recognition is well established, as the natural habitat of *Campylomormyrus* has extremely low-light conditions due to the high-level of suspended particulate matter and turbidity in the system (Stiassny and Alter 2015), in addition to our species being nocturnal. Recent studies showed that nocturnal weakly electric fish perceive electric colors for fast and reliable prey recognition (Gottwald et al. 2018). It has been shown that snout morphology and EOD characteristics are correlated, such that long putatively derived EODs are exhibited by long snouted species (Tiedemann et al. 2010). It is however unknown whether this diversification in snout morphology and EOD is functionally correlated or just coincidental. Whether the EOD functions as a "magic trait" (i.e. whether the elongated EOD serves both as a prezygotic isolation mechanism and is functionally related to foraging specialisation, as suggested by Feulner et al. 2009a, b) remains hence to be elucidated.

One should also take into consideration the phylogenetic framework of our study. In fact, *C. compressirostris* and *C. rhynchophorus* are closely related, while the short snouted *C. tamandua* stands phylogenetically apart (Lamanna et al. 2016). As *C. compressirostris* and C. *rhynchophorus* are closely related and significantly differ in both snout length and substrate preference, divergent snout evolution in an ecological speciation context seems a plausible scenario for these species (Feulner et al. 2008; Tiedemann et al. 2010), while further adaptations may have contributed to the divergence of the more distant lineages.

Conclusions

In conclusion, the present results support the hypothesis that *Campylomormyrus* species have undergone ecological speciation. In particular, the diversification of the feeding apparatus may be triggered by niche partition, to reduce interspecific competition. The study proposes that the diversification of snout morphology in African weakly electric fish is potentially driven by the adaptation to foraging on different substrates. Snout morphology may be under disruptive natural selection and play a role in niche segregation. Furthermore, in the natural habitat substrates are not randomly distributed. The lower Congo rapids at Kinshasa/Brazzaville comprise stony habitats with different gravel size, while right upstream of the rapids, the substrate is sandy (pers. observation). Substrate preferences may hence render species currently considered sympatric in the lower Congo rapids area to actually exhibit a microallopatric occurrence.

Availability of data and material

All data analysed during this study are included in this article as supplementary information files. Custom MatLab scripts are available from the authors upon request.

Compliance with ethical standards

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

Ethical approval and consent to participate Authors confirm that the Deputy for Animal Welfare of the University of Potsdam approved the experiments reported here and that all experiments were in accordance with relevant national guidelines and regulations.

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