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Asymmetric Jaw Morphology in an Herbivorous Cichlid from Lake Malawi

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in Biology with Honors

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APPROVED

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Abstract

Cichlid fish exhibit a high frequency of variation across species. This study focused on a particular asymmetry in the jaws of fish in the genus *Tropheops*. An asymmetry towards the left side was observed and then tested. Each side of the jaw was measured in a number of individuals from different *Tropheops* species. These measurements were then analyzed to see if the left side was indeed longer than the right. Statistical analysis was utilized to test the significance of sided differences. It was found that *Tropheops* species exhibit a left sided bias, some species having a significant bias, and others showing a leftward trend. Two other species, *Labeotropheus fuelleborni* and *Cyanotilapia afra*, were tested for comparison to see if this leftward trend is specific to *Tropheops* species. These species did not have a significant bias, but did show a trend toward a longer left side. It is predicted that the pronounced asymmetry in *Tropheop* jaw morphology is reflective of methods of food collection and diet.

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Introduction

Nature abounds with examples of anatomical asymmetries, some of which are fixed across multiple species, while others have evolved in just a few groups, and others arise due to malfunctions during normal embryological development. An example of a fixed anatomical asymmetry is the asymmetric positioning of the internal organs. This asymmetric positioning is fixed in all vertebrate species, and is what allows our organs to fit within a relatively small body cavity. Evolved asymmetries usually involve the appearance of an anatomical asymmetry in a normally paired structure. For example in several owl species the external ears are asymmetric. The ear is usually larger and positioned above the horizontal plane on one side of the head, whereas it is smaller and positioned below the horizontal plane on the other side. This asymmetry is believed to aid in prey location at night (Payne 1970). Male narwhals also exhibit evolved asymmetries, as they usually have one tusk emerging from the left side of the head. Only 1.5% exhibit double tusks, and in these cases the left tusk is longer (Hay 1984). The purpose of this asymmetry remains a mystery. Many human birth defects are characterized by the asymmetrical development of facial features, including unilateral cleft palate, Treacher Collins Syndrome, and Hemifacial Microsomia. Asymmetries also carry social implications, as a recent study indicated that human facial asymmetry is negatively correlated with judgments of attractiveness (Scheib 1999). While considerable progress has been made toward understanding the developmental origins of fixed asymmetries (i.e., positioning of the internal organs), there is much less known about the developmental or genetic

mechanisms that lead to the asymmetrical evolution of normally symmetrical structures. The focus of this paper is on the evolution of directional biases in the lower jaws of cichlid fish.

Cichlids were chosen as the subject of the study for several of reasons.

Cichlid fish, in general, exhibit extensive morphological variation. These fish are found in large lakes in Africa, where there was basically an explosion of evolution. There are around 1500 species of cichlids in this region. This raises the question of how such diversity has evolved in this particular group of fish. One genus of cichlids from Lake Tanganyika, *Perissodus*, contains specialized scale-eaters that have evolved asymmetries in their jaws to aid them in predation. They sneak up from behind prey fish and ram their flanks with open mouths in order to strip scales from their sides. *Perissodus* species are able to attack fish from behind (instead of approaching from the side) because



Figure 1: From top; (different species, drawing of *Tropheops*.)

their jaws are positioned at an angle. Interestingly, the different forms, right or left, are maintained within a population by frequency-dependent selection (Hori, 1993), because individuals with the rare jaw form have an advantage when feeding. As “lefty” or “righty” jawed individuals increase in frequency over time, prey will be attacked more frequently from one side. The prey will then become more cautious of attacks on that side, decreasing the success of attacks from the predominant jaw-type, while the small group of predators attacking the opposite side will see an increase in success (Hori, 1993).

This study focused on a different genus of cichlids, *Tropheops*, which is an herbivorous species. Preliminary observations of the lower jaw seemed to show that these fish have a directional bias in the length of one side, usually the left. According to Albertson (2008), the shape of the lower jaw has a close association with feeding performance of bony fishes. There is a high occurrence of specific niche partitioning among species of cichlids characterized by both morphological differences and differences in feeding behaviors. *Tropheops* species are characterized by a steeply descending snout and a slightly sub-terminal mouth. They typically feed from the rocky substratum while oriented 45° to the substrate and utilize a sideways and upward jerking motion, referred to as ‘nipping,’ when feeding (Ribbink et al., 1983; Reinthal, 1990a). This study will explore the possibility that the directional bias in jaw length could be related to this sideways motion of feeding by comparing *Tropheops* jaw laterality to that in species that employ modes of feeding that do not involve lateral (sideways) movements. *Labeotropheus fuelleborni* is another herbivorous species that crops attached

algae from the substrate while feeding parallel to the rocky surface. *Cyanotilapia afra* is a planktivorous species that forages in the water column by sucking plankton into their mouths. We expect that neither of these species will show jaw asymmetries. The major goals of this study are to quantify the magnitude and direction of the asymmetry in the cichlid lower jaw, and relate this asymmetry to the foraging strategies of different cichlid species.

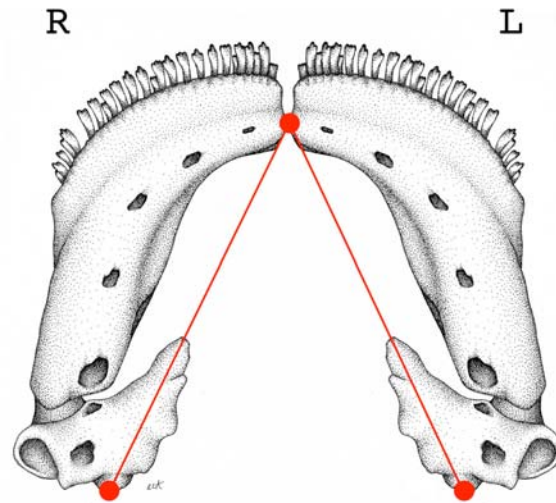


Figure 2: Ventral view of *Tropheops* jaw. Red dots indicate landmarks; red lines show measurements of right and left side lengths.

Methods

Digital photographs were taken of the ventral side of the lower jaw. Landmarks were placed on the computer as shown in Figure 2, and these were used to measure the lengths of the left and right sides. Once calculated, the right side was

subtracted from the left side to see which was longer. In this

case any positive values indicated a longer left side, and negative values indicated a longer right side. Chi square goodness of fit tests were used to compare the number of left versus right jawed individuals against an expected ratio of 1:1 to see if there was a significant bias. Paired T-tests were then utilized to assess whether there was a difference in the means of each side of the jaw. An index of asymmetry was also calculated for comparison using the formula $L/L+R$ (according to Hori et al., 2007). The results of this calculation are that any value higher than 0.5 indicates an individual with a longer left side. These calculations were then presented in histograms as index of asymmetry versus frequency as a percentage. Twelve species of *Tropheops* were measured, 283 individuals in all. These species include *T. gracilior*, *T. 'black dorsal'*, *T. 'orange chest'*, *T. microstoma*, *T. chinyankwazi*, *T. lilac*, *T. 'gold'*, *T. 'red cheek'*, *T. zimbawe*, *T. chinyamwezi*, and *T. 'intermediates'*. In order to see whether the results were

specific to *Tropheops*, and whether feeding mode is an important factor, two other species, *Labeotropheus fuelleborni* (8 individuals) and *Cyanotilapia afra* (17 individuals) were measured for comparison.

Results

Based on the statistical analysis, the asymmetry measured among all *Tropheops* species was significant and biased to the left side. The p-value found using the chi squared test was less than 0.005 (Table 1), and for the t-test it was equal to 0.003 (Table 2), which are both significant. The bias is also apparent in the histogram (Figure 3). Only ~25% of individuals had a symmetric jaw, whereas over 65% had a longer left side and only ~10% had a longer right jaw.

Labeotropheus and *Cyanotilapia* did not show a significant asymmetry but did exhibit a trend toward the left side of the jaw being longer. The p-values for *Labeotropheus* were 0.5 (Table 1) and 0.134 (Table 2), which are not significant. The p-values for *Cyanotilapia* were 0.8 (Table 1) and 0.995 (Table 2) which are highly insignificant. The trend to the left in both species is visible in the histograms (Figure 3), although it is much less apparent than in *Tropheops*. For *Labeotropheus*, ~45% had symmetrical jaws, ~55% had a longer left side. There was not much variation in side lengths, and they did not differ much from symmetrical lengths. For *Cyanotilapia* a little less than 50% were symmetrical and a little more than 50% had a longer left side, and like *Labeotropheus* there was not much variation in side lengths, and lengths did not stray far from symmetry.

Results across individual species of *Tropheops* were fairly consistent. Seven out of the twelve species had significant t-test results, and all but one species showed a trend towards a longer left side. *T. gracilior* showed a bell curve around symmetrical (0.5) when its indexes of asymmetry were graphed (Figure

4). *T. lilac* was an interesting case because it showed a large degree of variation in jaw asymmetries. There was a slight trend towards the left but not significant. *T. chinyankwazi* was an example of a species that did not show significant results, but did show a trend towards a longer left side. It would be interesting to know whether these anatomical differences in laterality relate to differences in diet or feeding behaviors between these *Tropheops* species.

Table 1: Results of chi squared goodness of fit tests.

<i>Tropheops</i>			<i>Labeotropheus</i>		
	L>R	R>L		L>R	R>L
Observed	188	95	Observed	5	3
Expected	141.5	141.5	Expected	4	4
X ²	30.56184		X ²	0.5	
Df	1		df	1	
P	<.005		P	~0.5	

<i>Cyanotilapia</i>		
	L>R	R>L
Observed	9	8
Expected	8.5	8.5
X ² =	0.058824	
df=	1	
p =	0.8	

Table 2: Two tailed T-Tests

	n	T-Statistic	P-Value
<i>Tropheops</i>	283	2.903	0.00397
<i>Cyanotilapia</i>	17	0.0062	0.995
<i>Labeotropheus</i>	16	1.5827	0.134

Figure 3: Histograms of index of asymmetry for *Tropheops*, *Labeotropheus*, and *Cyanotilapia*.

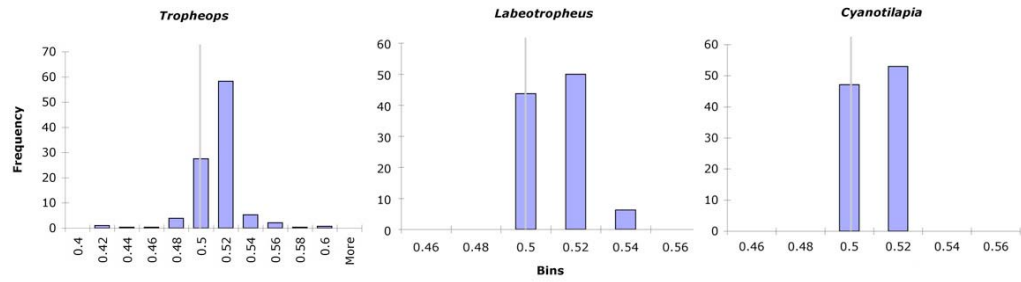
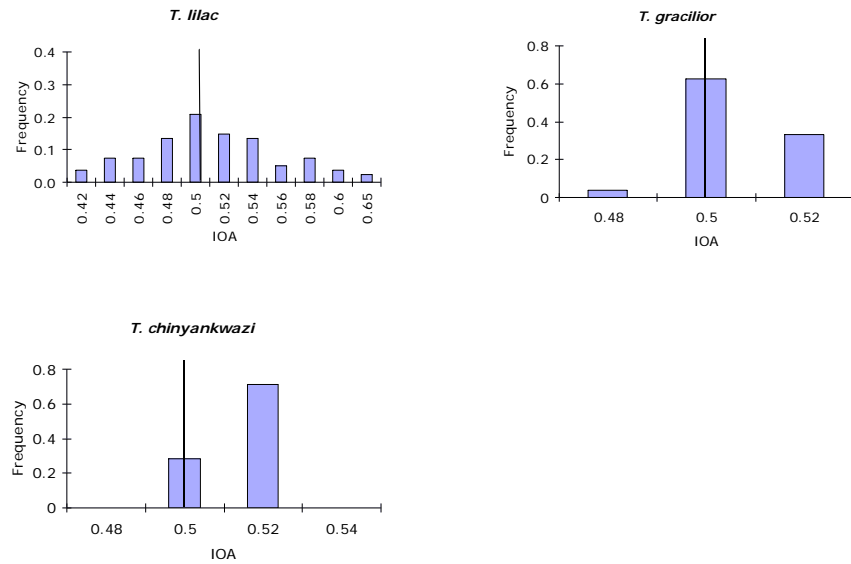


Figure 4: Histograms of *Tropheops* species *T. lilac*, *T. gracilior* and *T. chinyankwazi*.



Discussion

Tropheops showed a significant bias to the left side, as shown in the histograms as well as through the statistical analyses. *Cyanotilapia* and *Labeotropheus* did not show significant bias but did show a trend towards the left (Figure 3) which is interesting. Since all groups show a common tendency towards a longer left side, this could indicate a natural bias in jaw laterality. In a genetic study it was shown that when a key developmental gene is knocked out in the zebrafish, mutants are characterized by asymmetric bone development where right sided elements are missing more often than those on the left (Albertson 2005). These data are consistent with an inherent asymmetry of jaw development.

To further explore the possibility of jaws being naturally biased to one side, we need to look at how this inherent bias could be formed. Asymmetry is seen early on in the development of many organisms. It has been found that in all vertebrates, asymmetric development is initiated by the clockwise rotation of cilia found within a ball of cells at the embryonic midline. This ciliary movement sets up a leftward flow of fluid, which may cause a (so far undiscovered) signaling molecule to be pushed towards the left side of the embryo. Regardless of the specific mechanism, this ciliary movement leads to (and is required for) the expression of the signaling molecule Nodal on the left side of the developing embryo. Nodal signaling is universally conserved in cephalochordates, tunicates, echinoderms, and vertebrates, and is the first sign of asymmetric development in vertebrates (Capdevila 2000). This signal ultimately leads to the asymmetric development of the internal organs (i.e., heart, stomach and pancreas) and brain.

Interestingly, early stages of jaw development also occur at this time. Specifically, the jaws are developing at a time when Nodal is expressed on the left side of the embryo, and thus are being formed in a fundamentally asymmetric environment. Understanding these early asymmetric signals and how they interact may give clues as to how superficially paired structures can evolve laterality.

Interestingly, the earliest stages of tooth and ear development are also coincident with asymmetric Nodal signaling. Examples of asymmetries favoring the left side in these areas have been observed in narwhals and owls. As previously mentioned, male Narwhals tend to grow a long tusk on the left side. It is unknown why this occurs though, and does not seem to show an advantage in natural selection. In the barn owl, the left ear is higher than the right ear. In this case the asymmetry gives the owl an advantage because it can better locate prey at night depending on which ear receives a louder signal. It's possible that these asymmetries evolve due to an accentuation of the developmental favoritism described above.

Comparing *Labeotropheus* and *Cyanotilapia* data to those from *Tropheops* shows a combination of developmental favoritism and evolutionary benefit. All three groups showed a trend towards the left, but the fact that *Labeotropheus* and *Cyanotilapia* did not show a statistically significant bias, while *Tropheops* did might be due to differences in feeding mode. *Cyanotilapia* species use suction to feed on plankton, while *Labeotropheus* bite attached algae from the substrate. Both genera approach their food straight-on. *Tropheops*, however, use a sideways mode of feeding. They approach algae and nip by jerking to one side (Reinthal,

1990). This may indicate an advantage to having an asymmetric jaw, and thus why *Tropheops* evolved a significant bias to the left side. Further studies could be done see if *Tropheops* tend to nip to one side when feeding, and to assess the degree to which asymmetric foraging behaviors correlate with asymmetric feeding morphologies since certain *Tropheops* species are more asymmetric than others. If this is the case it may contribute to the persistence of an asymmetrical jaw through natural selection. Given the variation among *Tropheops*, it is possible that certain *Labeotropheus* and *Cyanotilapia* species will show more dramatic asymmetries. This possibility is less probable though as the feeding behavior in *Labeotropheus* and *Cyanotilapia* is highly conserved among species, whereas it is highly variable among *Tropheops* species (Albertson 2008). However, these species would continue to provide a good comparison to the variation seen in *Tropheops*.

Studying the variation within *Tropheops* species may show this combination of developmental and evolutionary favoritism as well. As a whole, all thirteen species showed a significant bias to the left, but when analyzed as individual species, some groups showed significance and others did not. The species *T. lilac* showed results that greatly varied from the rest, as there was not a bias to one side, but there was a significant degree of variation in jaw asymmetry. Other species, such as *T. chinyankwazi* and *T. gold* did not show significant results, but like *Labeotropheus* and *Cyanotilapia*, they showed a trend towards the left side, which may be due to the natural leftward bias we predict. Future research should look for an association between degrees and direction of asymmetry and benefits

to foraging across *Tropheops* species. Observations of differences in their diets and modes of food collection should be taken, as my research has found an association between jaw laterality and laterality in feeding behavior. The hypothesis would be that certain *Tropheops* species possess a left sided bias in their jaw due to a greater affinity towards laterality in feeding behavior.

Conclusion

Tropheops species, as well as *Labeotropheus fuelleborni* and *Cyanotilapia afra* all exhibited some degree of asymmetry in their jaw. While some only showed a trend towards a longer left side, others showed a significant bias. This variation across cichlid species opens up the possibility of understanding the asymmetrical development of typically bilateral structures, a phenomenon observed in many organisms, including humans.

There are a multitude of other Lake Malawi cichlid species that feed in a variety of ways (including scale-eaters!), and it would be very interesting to know whether asymmetries in jaw morphology or feeding behavior exist in other groups. Given my data, and the hypothesis that jaw laterality is fundamentally biased, I predict that there is a good chance that other significant asymmetries will be found in the lake. The evolutionary significance and genetic basis for these will be topics of interesting future investigations.

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Capstone Summary

Nature abounds with anatomical asymmetries, some which are fixed across multiple species, while others have evolved in just a few groups, and others arise due to malfunctions during normal embryological development. An example of a fixed anatomical asymmetry is the asymmetric positioning of the internal organs. This asymmetric positioning is found in all vertebrate species, and is what allows our organs to fit within a relatively small body cavity. Evolved asymmetries usually involve the appearance of an asymmetry in a normally paired structure. There is still little known about the developmental or genetic mechanisms that lead to the asymmetrical evolution of previously symmetrical structures. The focus of this paper is on the evolution of asymmetry in the lower jaws of cichlid fish.

Cichlids were chosen as the subject of the study for several of reasons. First, they exhibit extensive variation in size, structure, and color. These fish are predominantly found in large lakes in East Africa, where there was basically an explosion of evolution of new species. There are around 1500 species of cichlids in this region. This raises the question of how so much diversity has evolved in this particular group of fish. One group of cichlids from Lake Tanganyika includes specialized scale-eaters that have evolved jaws with one side longer than the other. This aids them in feeding. They sneak up behind their prey and ram their sides with open mouths in order to strip scales from their flanks. They are able to use this “ambush” hunting strategy in part because their jaws are asymmetrically positioned to the left or right side.

This study focused on a different group of cichlids, members of the genus *Tropheops*, which are primarily herbivorous species. Preliminary observations of the lower jaw seemed to show that one side was longer than the other, usually the left. According to Albertson (2008), the shape of the lower jaw has a close association with the method used to feed. *Tropheops* species are characterized by a steeply descending snout and a slightly sub-terminal mouth. They typically feed from the rocky substratum while oriented 45° to the substrate and utilize a sideways and upward jerking motion, referred to as ‘nipping,’ when feeding (Ribbink et al., 1983; Reinthal, 1990a). My study explores the possibility that the directional bias in jaw length could be related to this sideways motion of feeding by comparing *Tropheops* jaws to fish that feed straight-on. *Labeotropheus fuelleborni* is another herbivorous species that crops attached algae from the substrate while feeding parallel to the rocky surface. *Cyanotilapia afra* is a planktivorous species that forages in the water column by sucking plankton into their mouths. We expect that neither of these species will show jaw asymmetries. The major goals of this study are to measure the magnitude and direction of the asymmetry in the cichlid lower jaw, and relate this asymmetry to the feeding strategies of different cichlid species.

Digital photographs were taken of the ventral side of the lower jaws of various *Tropheops* species, as well as of *Labeotropheus fuelleborni* and *Cyanotilapia afra*. These images were used to measure the lengths of the left and right sides of the lower jaw. These lengths were then entered into an excel spreadsheet and analyzed statistically to test which groups of fish had a significant asymmetry in

their jaw. *Tropheops* showed a considerable bias to the left side. *Cyanotilapia* and *Labeotropheus*, on the other hand, did not show significant asymmetry but did show a trend towards the left side being longer. Since all groups showed a common tendency towards a longer left side, this could indicate a natural bias in jaw shape. This is interesting because in a genetic study it was shown that when a key developmental gene is knocked out in the zebrafish, mutants are characterized by asymmetric bone development where the right sided elements are missing more often than those on the left (Albertson 2005). These data are consistent with an inherent asymmetry of jaw development.

A further look shows that certain key signals are active on the left side of the embryo. In all animals, asymmetry is initiated early in development by the clockwise rotation of cilia in a small organ at the midline of the embryo. This rotary movement is thought to set up a leftward flow of fluid, which then activates a cascade of expression of various growth factors on the left side of the embryo. This ultimately leads to the asymmetric development of the internal organs and brain (i.e., heart, stomach and pancreas). Interestingly, early stages of jaw development also occur at this time. Specifically, the jaws are developing at a time when the left-right axis is being determined, and thus are being formed in an asymmetric environment. Understanding these early asymmetric signals and how they interact with other developmental programs may give clues to the left sided bias we have observed in the jaws.

The fact that *Labeotropheus* and *Cyanotilapia* did not show a statistically significant bias, while *Tropheops* did, might be due to differences in feeding

mode. As mentioned previously, *Cyanotilapia* use suction to feed on plankton and *Labeotropheus* feed straight on relative to the substrate. *Tropheops* however use a sideways jerking mode of feeding. They approach algae and nip by jerking to one side (unpublished observations). Having an asymmetric jaw may provide an advantage during this type of feeding, and could explain why *Tropheops* species have evolved a significant bias to the left side. Further studies should be done to carefully observe the feeding of *Tropheops*, in order to see if they tend to nip to one side when feeding. If this is the case it may contribute to the persistence of asymmetrical jaws through natural selection.

Some other species express left sided asymmetries as well. One example is the Narwhal. The male Narwhal tends to grow a long tusk on the left side. Only 1.5% exhibit double tusks, and in these cases the left is the longer tusk (Hay 1984). It is unknown why this occurs though these tusks do not seem to provide an ecological advantage. Since females do not generally have tusks, this may be a sexually selected trait. In the barn owl, the left ear is higher and generally larger than the right ear. This gives the owl an advantage because it can tell if a sound emanates from above or below itself depending on which ear receives a louder signal, which allows owls to better locate prey while hunting at night. In both owls and narwhals (like cichlids), the left-sided bias of these anatomical asymmetries might be linked to an inherent left-sided bias of development. Further study of asymmetry is also of interest because many human birth defects are characterized by the asymmetrical development of facial features, including unilateral cleft palate, Treacher Collins Syndrome, and Hemifacial Microsomia.

Asymmetries also carry social implications, as a recent study indicated that human facial asymmetry is negatively correlated with judgments of attractiveness (Scheib 1999). Our work with cichlids will facilitate an understanding of how these widespread asymmetrical mysteries develop and evolve.