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Functional significance of variation in trophic morphology within feeding microhabitat-differentiated cichlid species in Lake Malawi

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Abstract—Shape variation in trophic morphology between species in two trophic guilds (zooplankton and epilithic algal feeders) was investigated using landmark-based geometric morphometrics. Three disarticulated bone elements from the head region were examined; the neurocranium, the premaxilla and lower jaw. From separate analyses of each bone element, significant shape variation was identified between species in each trophic guild. The deformation grids generated revealed that, for the zooplankton feeders, *Ctenopharynx pictus* has a longer neurocranium, a longer and ventrally directed vomer, a larger orbit, a shorter ascending arm, a shorter maxillad spine, and a more compressed articular bone relative to *Copadichromis borleyi.* In algal feeders, *Labeotropheus fuelleborni* has a shorter neurocranium, a smaller orbit, a ventrally directed vomer, a longer ascending arm, a shorter dentigerous arm, increased height of the articular process, and a more elongated dentary than *Petrotilapia genalutea.* Observed anatomical differences are discussed in terms of function, specifically with respect to the feeding microhabitat differentiation between species in each trophic guild. These differences enable us to appreciate the role that trophic morphology plays in enhancing ecological segregation, leading to coexistence of the species.

Keywords: algal feeders; Cichlidae; geometric morphometrics; thin-plate spline; zooplankton feeders

INTRODUCTION

In the East African Great Lakes, viz. Victoria, Tanganyika and Malawi, many cichlid species are known to coexist in high densities along the rocky shores. Such coexistence is frequently attributed to the manner in which these cichlids partition

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resources through temporal, spatial and trophic means (Ribbink et al., 1983; Witte, 1984; Bouton et al., 1997). Trophically, cichlids are known to segregate along various niche axes including: food size partitioning, quantitative differences in food composition, differences in food collecting strategies, and partitioning of feeding microhabitats (Yamaoka, 1982, 1997; Hori, 1983, 1991; Witte 1984; Goldschmidt, 1990; Reinthal, 1990; Yuma, 1994; Kohda and Tanida, 1996; Genner et al., 1999a, b). In most cases, these trophically segregated groups can be identified by structural differences in their trophic morphology, even though such differentiation is related more to the way the food is captured and processed than to the type of food consumed (Barel, 1983; Yamaoka, 1997). The key to trophic segregation in cichlids appears to be the diversification of the oral jaw apparatus that has enabled cichlids to evolve specialised modes of feeding, and to utilise almost all available feeding niches.

In Lake Malawi, many cichlid species coexist along the rocky shores (e.g., 15 species at West Thumbi island, our collection site; Ribbink et al., 1983). To understand fully what mechanisms promote the coexistence of these species, the role of morphological variation within and between species must be investigated. Some studies have begun to investigate this (e.g. Reinthal, 1989; Kassam et al., 2002 a, b). Kassam et al. (2003a) examined the role of body shape in resource partitioning among four species coexisting along Lake Malawi's rocky shores: *Copadichromis borleyi* and *Ctenopharynx pictus* (zooplankton feeders), and *Labeotropheus fuelleborni* and *Petrotilapia genalutea* (epilithic algal feeders). These species are segregated along a food axis, and are segregated spatially in terms of feeding microhabitat. *Ctenopharynx pictus* is mainly benthophagous, but also feeds from the water column when zooplankton is in abundance (T. Sato, pers. comm.), while its counterpart, *Copadichromis borleyi,* is reported to feed from the open water (Ribbink et al., 1983; Konings, 1990). The two algal feeders inhabit shallow rocky areas, but *L. fuelleborni* is commonly found on the sediment-free wave-beaten sides of the rocks (Ribbink et al., 1983; Konings, 1990). Kassam et al. (2003a) found that the head region was most morphologically divergent among these species. This finding prompted us to investigate further what specific anatomical features may be responsible for the observed variation in head shape. We therefore, analysed several bone elements in the head region: the neurocranium, the lower jaw and the premaxilla in the upper jaw. The neurocranium was included because of the role it plays in conjunction with the oral jaws through the ethmovomer region (Reinthal, 1989; Yamaoka, 1997; Albertson and Kocher, 2001).

The goal of our study was to examine patterns of shape variation in these anatomical elements between species in each trophic guild, and determine whether the observed morphological patterns relate to resource partitioning (especially feeding microhabitat differentiation), in an attempt to understand the role that trophic morphology plays as a mechanism promoting species coexistence.

MATERIALS AND METHODS

Specimen preparation

Specimens ($n = 20$ per species) used in this study were collected from West Thumbi Island as described in Kassam et al. (2003a). The following species were used: *Copadichromis borleyi* (standard length, SL, 80.5-127.5 mm), *Ctenopharynx pictus* (SL, 78.6-101.3), *L. fuelleborni* (SL, 81.7-104.2) and *P. genalutea* (SL, 85.9-116.4). We used Potthoff's (1984) protocol to clear and stain all bones in the head region. Drawings of all anatomical structures were made using a Leica-MS 5 microscope attached to a camera lucida. These were later scanned and digitised for geometric morphometric analysis. Osteological nomenclature follows that of Barel et al. (1976).

Geometric morphometrics and statistical analyses

Following Albertson and Kocher (2001), we focused on individual skeletal elements, which enables us to reveal patterns of morphological variation that are otherwise obscured if articulated skeletons or external morphology alone is considered. Quantification of the shape of each disarticulated bone structure (neurocranium, premaxilla and lower jaw) was done using landmark-based geometric morphometrics (GM) methods (Rohlf and Marcus, 1993). First, TPSDIG32 (Rohlf, 2001) was used to digitise the locations of biologically homologous landmarks on the lateral side of each bone structure (fig. 1). For the neurocranium, the following landmarks were recorded (fig. 1a): 1) rostral tip of the vomer; 2) caudal-most point of the preorbital ridge; 3) dorsal tip of the suppraoccipital crest; 4) ventral process of the vertebrad concavity; 5) pharyngobranchiad apophysis; 6) tip of postorbital process; 7) tip of preorbital process; 8) caudal-most point of the vomerine-palatinad articulation facet. For the premaxilla, five landmarks were recorded (fig. 1b): 1) dorsal process of the ascending spine; 2) rostro-most point of the dentigerous arm; 3) caudal process of the dentigerous arm; 4) dorsal process of the maxillad spine; 5) ventro-most point of the interprocess edge. Finally, eight landmarks were recorded from the lower jaw (fig. 1c): 1) rostral tip of the dentary; 2) dorsal tip of the coronoid (dentary) process; 3) dorsal tip of the primordial (articular) process; 4) dorsal process of the suspensoriad articulation facet; 5) postarticulation process (of the suspensoriad articulation facet); 6) retroarticular process; 7) rostral process of the coulter area; 8) tip of the rostral process of the articular. These landmarks were chosen for their capacity to represent prominent features and to capture the overall shape and structure of each bone.

For all subsequent analyses, the landmark coordinates from each bone were treated separately. First, all specimens were superimposed using the Generalised Procrustes Analysis (GPA) (Rohlf and Slice, 1990) to remove non-shape variation arising from differences in scale, orientation and translation. From the GPA aligned specimens, shape variables were obtained by generating partial warp scores and uniform components using the thin-plate spline and standard uniform equations

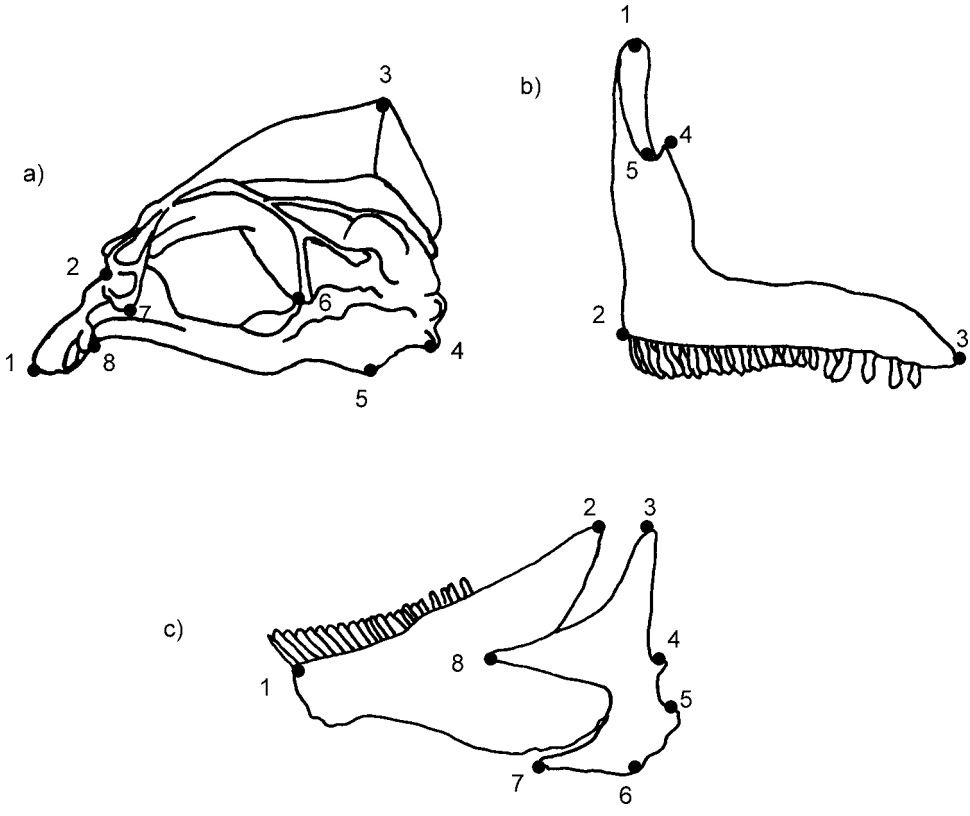


Figure 1. Landmarks collected on each skeletal element; a) neurocranium, b) premaxilla, c) lower jaw. The landmarks are defined in Material and Methods section.

(Bookstein, 1989, 1991, 1996). Together, the uniform and non-uniform components are treated as a set of shape variables for statistical comparisons of shape variation within and among groups (see e.g., Caldecutt and Adams, 1998; Adams and Rohlf, 2000; Rüber and Adams, 2001; Kassam et al., 2003a, b). In addition to this analysis, the specimens for each species were superimposed separately using GPA, and the average (consensus) configuration of landmarks was obtained. These mean specimens were then compared to the overall consensus configuration (reference) to visualise shape variation among species using thin-plate spline deformation grids. TPSRELW software (Rohlf, 2002) was used to perform all these analyses.

To identify any shape variation among species, a Canonical Variate Analysis (CVA) was performed on the weight matrix of shape variables (partial warp scores and uniform components of shape). This analysis was performed separately on the shape data for each bone. When the multivariate analysis of variance (MANOVA) identified significant differences among species, pairwise multiple comparisons using generalised Mahalanobis distance (D^2) were performed to determine which species differed from one another (after Bonferroni adjustment). The CVA analyses were performed in NTSYS-PC (Rohlf, version 2.1, 2000).

Table 1.
Pairwise comparisons for the three bone elements, based on Mahalanobis distances: Upper value represents neurocranium, middle value is for premaxilla, and lower value is for lower jaw. ns depicts pairs not significantly different (after Bonferroni correction).

Species	*C. borleyi*	*C. pictus*	*L. fuelleborni*	*P. genalutea*
C. borleyi	0.0			
C. pictus	6.2	0.0		
	4.0			
	7.1			
L. fuelleborni	8.6	8.9	0.0	
	9.1	11.8		
	13.1	12.9		
P. genalutea	4.5 ns	5.3	7.9	0.0
	9.2	10.5	6.9	
	11.1	11.8	10.9	

RESULTS

For all disarticulated bone structures, MANOVA revealed significant differences among species (neurocranium: Wilks' $\lambda = 0.003997$, $F = 29.35$, $P < 0.0001$; premaxilla: Wilks' $\lambda = 0.002955$, $F = 76.48$, $P < 0.0001$; lower jaw: Wilks' $\lambda = 0.000289$, $F = 79.03$, $P < 0.0001$), and pairwise comparisons for each of the bone structures revealed significant differences between species within each trophic guild (Table 1).

Discrimination among species can also be interpreted by examining the patterns found in an ordination of specimens in shape space, using CV1 and CV2 as the ordination axes (fig. 2a, b, c). For all anatomical structures, the first CV axis clearly discriminates between algal feeders from zooplankton feeders (i.e. between trophic guilds) while the second CV axis discriminates species within trophic guilds, according to feeding microhabitat. The one exception to this pattern is found for the neurocranium where *P. genalutea* (algal feeder) partially overlaps with *Copadichromis borleyi* (plankton feeder), reflecting their similarity identified in the pairwise comparisons (Table 1).

To anatomically describe the shape variation revealed between species, we generated and examined thin-plate spline deformation grids for the average bone for each species. Among zooplankton feeders, *Ctenopharynx pictus* has a longer neurocranium, a longer and ventrally directed vomer, and a larger orbit, relative to *Copadichromis borleyi* (fig. 3a, b). Among algal feeders, *L. fuelleborni* has a shorter neurocranium, and a smaller orbit and ventrally directed vomer, relative to *P. genautea* (fig. 3c, d). The premaxilla in zooplankton feeders is characterised by an ascending arm, and a longer ascending spine and maxillad spine in *Copadichromis borleyi* relative to *Ctenopharynx pictus* (fig. 4a, b). In contrast, in algal feeders the ascending arm and ascending spine are longer, and the dentigerous arm shorter in *L. fuelleborni* relative to *P. genalutea* (fig. 4c, d). In general, zooplankton

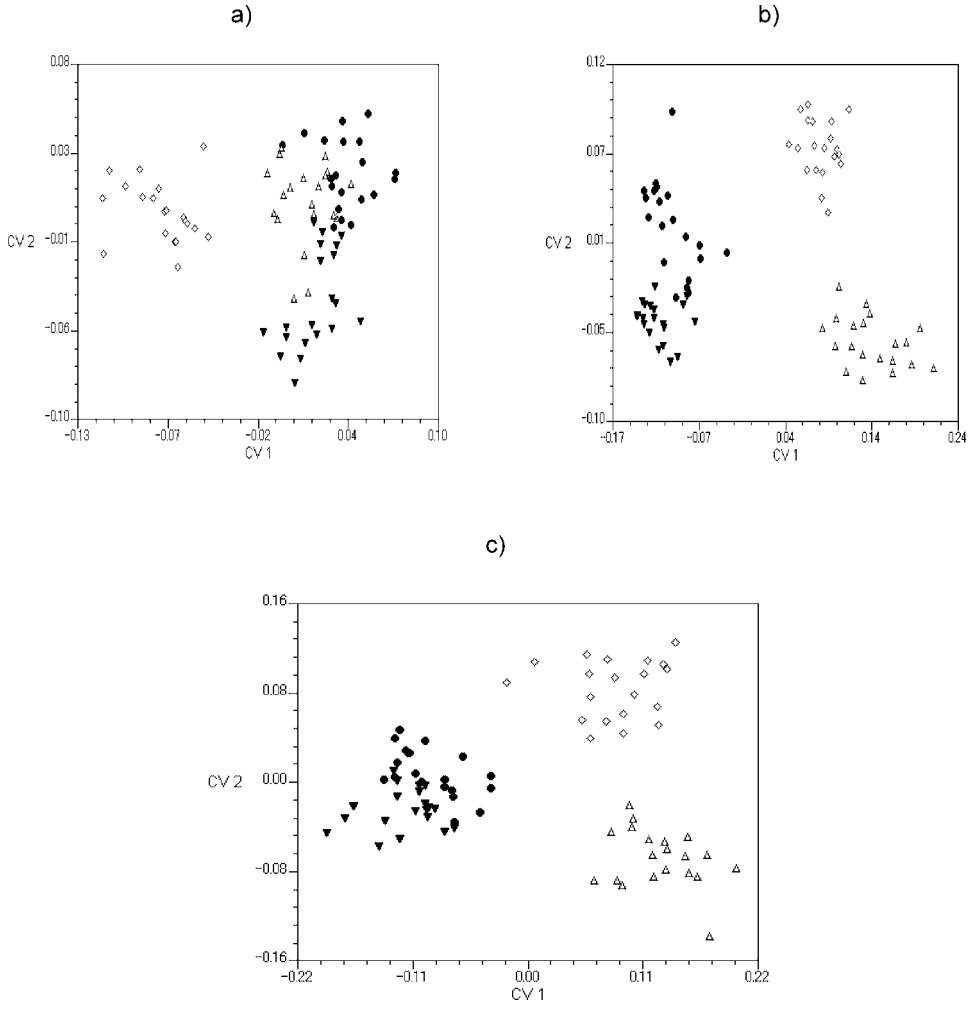


Figure 2. Ordination of specimens on the first two canonical variate axes; a) neurocranium, b) premaxilla, c) lower jaw. In all figures, filled circle (●) represents *Copadichromis borleyi*, filled down triangle (▼) is *Ctenopharynx pictus*, open diamond (◇) is *Labeotropheus fuelleborni*, and open up triangle (Δ) is *Petrotilapia genalutea.*

feeders possess longer ascending arms, shorter dentigerous arms, and shorter maxillad spines than algal feeders. Additionally, the angle between ascending and dentigerous arms is acute in zooplankton feeders, while obtuse in algal feeders (fig. 4). Comparing lower jaws between zooplankton feeders shows that the articular bone of *Ctenopharynx pictus* is more compressed than that of *Copadichromis borleyi* (fig. 5a, b), while for algal feeders, in *L. fuelleborni*, the articular process increases in relative height, there is a more elongated dentary, and a more concave suspensoriad articulation facet relative to that in *P. genalutea* (fig. 5c, d). Between

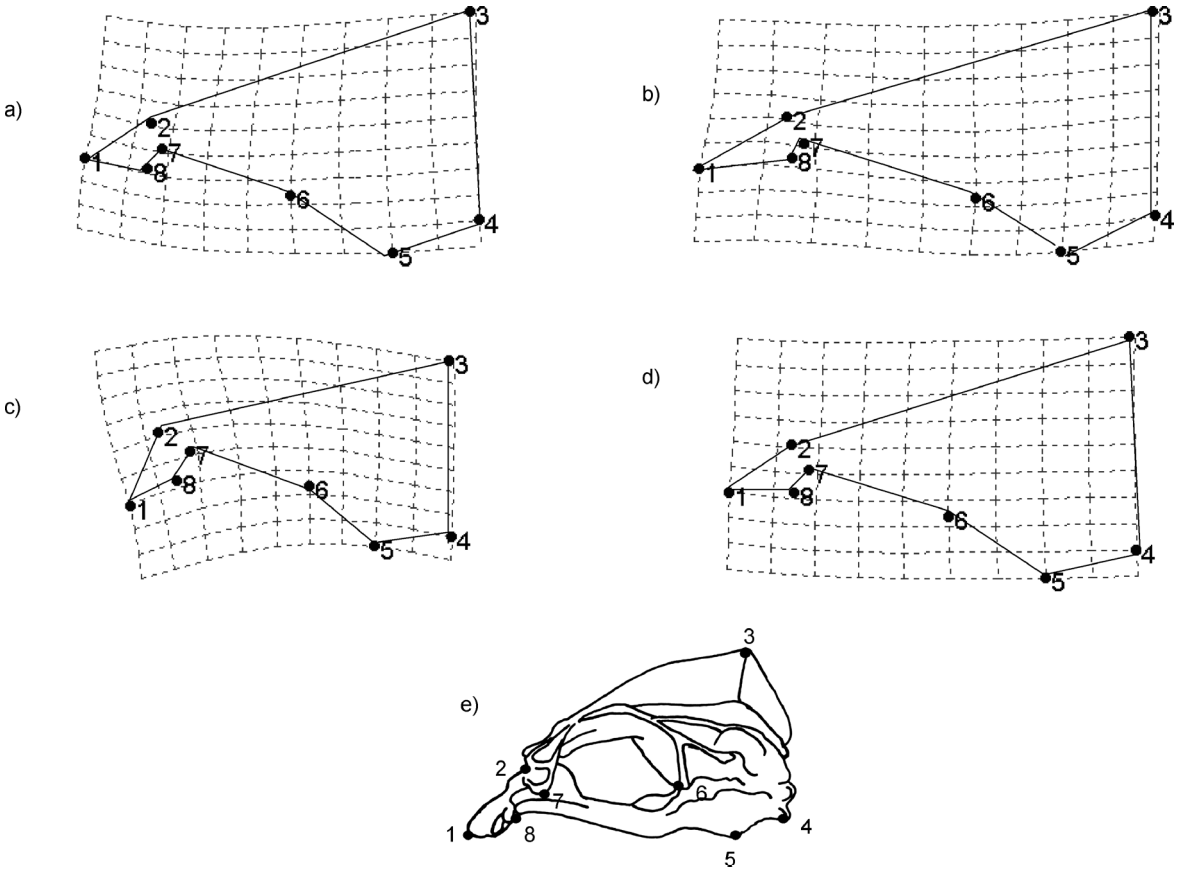


Figure 3. Deformation grids indicating neurocranium shape variation between consensus configurations for two zooplankton feeders; a) *Copadichromis borleyi*, b) *Ctenopharynx pictus*, and two algal feeders; c) *Labeotropheus fuelleborni*, d) *Petrotilapia genalutea*, e) neurocranium.

trophic guilds, the lower jaw tends to be more elongated and slender in zooplankton feeders than in algal feeders.

DISCUSSION

Using landmark-based geometric morphometric techniques, we quantified the shape of several anatomically important bones, and compared patterns of variation within and between trophic guilds of cichlid fishes. We revealed trophic morphological variation between species in each trophic guild (zooplankton and algal feeders). Among zooplankton feeders, it was found that *Ctenopharynx pictus* has a longer neurocranium, a larger orbit, a shorter ascending arm and maxillad spine, and a more compressed articular bone relative to *Copadichromis borleyi*. Among algal feeders, it was revealed that *L. fuelleborni* has a shorter neurocranium, a ventrally directed vomer, a longer ascending arm and spine, a shorter dentigerous arm, and an increased height of the articular process relative to *P. genalutea*. Some general features distinguishing the trophic guilds were also found; for instance, zooplankton feeders have longer ascending arms, shorter dentigerous arms, an acute angle between ascending and dentigerous arms, shorter maxillad spines, and more elongated and slender lower jaws relative to algal feeders. Because these structures are related to feeding, some of the observed differences in trophic morphology between species might reflect functional differences.

In terms of function, the role of the observed differences in trophic morphology between zooplankton feeders can be considered as follows: the longer neurocranium in *Ctenopharynx pictus* implies that the volume of its buccal cavity is greater, resulting in an attenuated and truncated cone capable of generating the high negative pressure required for suction feeding (Liem, 1991). Its larger orbit size is directly related to larger eyes, which concurs with the results from linear measurements of eye diameter for this species (Kassam et al., 2003a). All zooplankton feeders require large eyes (Fryer and Iles, 1972; Hart and Gill, 1994), since they have to visually select their prey (which tend to be small). However, Kassam et al. (2003a) hypothesised that the larger eyes in *Ctenopharynx pictus* enable the fish to obtain prey in a benthic environment, since this probably requires higher resolving power than obtaining prey in other habitats (as in *Copadichromis borleyi*). For *Copadichromis borleyi*, the longer ascending arm of the premaxilla suggests that this species can protrude its mouth to a greater extent than can *Ctenopharynx pictus*. Such a protruded mouth forms a tube-like structure that enables this species to suck individual prey from the water column into its mouth (Fryer and Iles, 1972; Greenwood, 1974).

The feeding mode and associated trophic morphology of *Copadichromis borleyi* is similar to that of a Lake Tanganyikan zooplankton feeder, *Gnathochromis permaxillaris* (see Fryer and Iles, 1972). Obtaining prey individually through suction feeding may not exist in *Ctenopharynx pictus* because it sucks in loose sediments on the bottom (from which prey is sieved), almost like a vacuum cleaner (Ribbink et

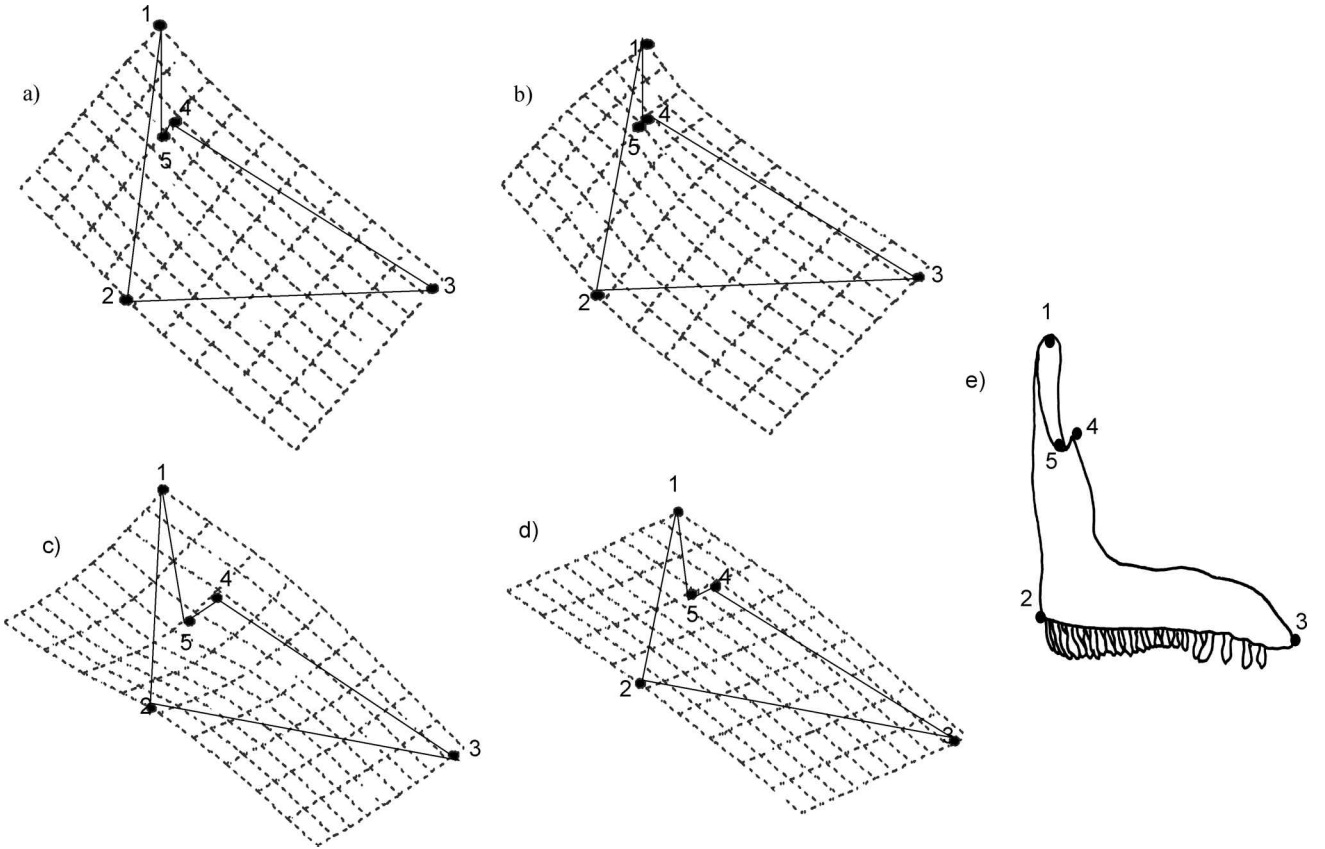


Figure 4. Deformation grids indicating premaxilla shape variation between consensus configurations for two zooplankton feeders; a) *Copadichromis borleyi*, b) *Ctenopharynx pictus*, and two algal feeders; c) *Labeotropheus fuelleborni*, d) *Petrotilapia genalutea*, e) premaxilla.

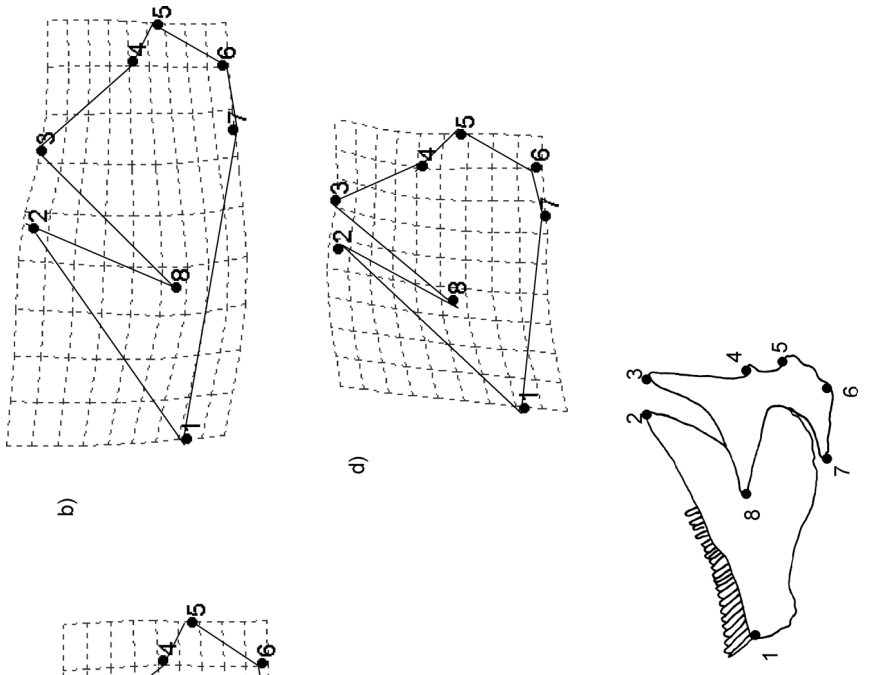


Figure 5. Deformation grids indicating lower jaw shape variation between consensus configurations for two zooplankton feeders; a) *Copadichromis borleyi*, b) *Ctenopharynx pictus*, and two algal feeders; c) *Labeotropheus fuelleborni*, d) *Petrotilapia genalutea*, e) lower jaw.

al., 1983). Unlike its counterpart, *Ctenopharynx pictus* does not form a long sucking tube, but can suck in large amounts of loose sediment because of its larger gape (Kassam et al., 2003a). Synthesising these findings, it is apparent that feeding microhabitat segregation, coupled with trophic morphological differentiation between these two zooplankton feeders, enhances ecological separation and possibly leads to their stable coexistence.

For the epilithic algal feeders, some patterns of trophic diversification may represent functional shifts in morphology. Yamaoka (1997) classified the Lake Tanganyikan epilithic algal feeders into two major trophic groups; browsers and grazers, of which the latter has three subgroups: combers, scrappers and suckers. Combers are fishes that comb unicellular algae, mainly diatoms, from filamentous algae (Yamaoka, 1997), whereas scrappers are fishes that scrape off epilithic algae (Yamaoka, 1987), and suckers refer to group of fishes that take mainly loose aufwuchs together with organic debris by using bucco-opercular cavity as a suction pump (Yamaoka, 1991). Yamaoka (1997) identified *Petrochromis fasciolatus* as a comber species and, because this is the ecomorphological equivalent to *Petrotilapia genalutea* (Kassam et al., 2003b), we conclude that *P. genalutea* is also a comber. Yamaoka (1997) also found that the neurocranium, and especially the vomer region, of the browser *Tropheus moorii* was very similar to that of *Labeotropheus fuelleborni* (fig. 2-15, Yamaoka, 1997). Additionally he found that members of these genera have ventrally directed mouths, and a very straight jaw margin, which extends transversely across the full width of the head (Fryer and Iles, 1972; Yamaoka, 1987). The ventrally directed mouth in *L. fuelleborni* was also identified by Kassam et al. (2003a), and in *T. moorii* by Yamaoka et al. (unpubl.). This resemblance in trophic morphology, coupled with the similar feeding habit displayed by the two species, allows us to infer that *L. fuelleborni* is also a browser.

Because *L. fuelleborni* is a browser and *P. genalutea* is a comber, the two species have a marked differentiation in feeding habit: a crucial factor in enhancing their ecological separation. This is consistent with earlier work showing that understanding the mechanisms of resource partitioning in fishes is best done through identifying how and where a fish feeds, rather than determining what food items are actually consumed (Smith and Tyler, 1973; Barel, 1983; Yamaoka, 1997).

The ventrally directed and well-developed vomer in *L. fuelleborni* is therefore suggested to have a similar function to that in *T. moorii*, namely, to provide a base for the powerful jaw biting mechanism (Yamaoka, 1997). The fact that *L. fuelleborni* feeds while its body is aligned horizontally/parallel to the substrate (Ribbink et al., 1983; Albertson and Kocher, 2001) is also in accord with this finding. The horizontally directed vomer in *P. genalutea* may reflect the fact that this species rostrally protrudes its mouth and combs filamentous algae while the body is perpendicular to the substrate.

Considering the lower jaw, the most pronounced variation between *L. fuelleborni* and *P. genalutea* is on the articular process which is higher in the former than the latter. In terms of function, Otten (1983) found that the articular process acts as

a vital lever in the jaw adduction because the second adductor mandibulae inserts on it. Thus, the higher articular process in *L. fuelleborni* implies that this species can generate a greater force, resulting in a stronger bite (Albertson and Kocher, 2001; Albertson et al., 2003), whereas the shorter articular process in *P. genalutea* implies that its jaw can close faster during the combing process. Fast jaw closing is consistent with what Yamaoka (1983) found in *P. fasciolatus*, an ecomporphological equivalent of *P. genalutea*, which showed the highest grazing speed among its congeners in Lake Tanganyika.

One of the generalisations made regarding differences in trophic morphology between zooplankton and algal feeders involves the angle formed between the ascending and dentigerous arms of the premaxilla. This angle is acute in zooplankton feeders and obtuse in algal feeders. Otten (1983) and Bouton et al. (1999) reported that the obtuse angle, as found in algal feeders, enables the fish to exert a greater force when biting.

In this study we found significant differences in the shapes of various bony elements of the trophic apparatus, both within and between trophic guilds. Examining each bone separately revealed shape differences in the individual anatomical elements of the trophic apparatus, which are obscured when the trophic apparatus is examined in an articulated fashion. Therefore, examining these elements individually can be a useful way of revealing potentially important functional anatomical differences among species. These findings compliment those of Kassam et al. (2003a), who found body shape variation among these species. Nevertheless, when trophic ecology is considered, it is likely that body shape alone cannot identify all of the potentially meaningful morphological variation within and among species. Therefore, an integrative approach that combines body shape and trophic morphological data is likely to provide the best explanation of morphological diversity in these cichlids. Such a pluralistic approach will enable us to appreciate the role that morphology plays in resource use and partitioning, so that we can better understand how these species coexist in nature.

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