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# Premaxillary movements in cyprinodontiform fishes: An unusual protrusion mechanism facilitates "picking" prey capture

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## Abstract

Premaxillary protrusion is hypothesized to confer a number of feeding advantages to teleost fishes; however, most proposed advantages relate to enhanced stealth or suction production during prey capture. Cyprinodontiformes exhibit an unusual form of premaxillary protrusion where the descending process of the premaxilla does not rotate anteriorly to occlude the sides of the open mouth during prey capture. Instead, the premaxilla is protruded such that it gives the impression of a beak during prey capture. We quantified premaxillary kinematics during feeding in four cyprinodontiform taxa and compared them with three percomorph taxa to identify any performance consequences of this protrusion mechanism. Individual prey capture events were recorded using digital high-speed video at 250–500 frames per second ($n \geqslant 4$ individuals, $\geqslant 4$ strikes per individual). Species differed in the timing of movement and the maximum displacement of the premaxilla during the gape cycle and in the contribution of the premaxilla to jaw closing. Cyprinodontiform taxa produced less premaxillary protrusion than the percomorph taxa, and were consistently slower in the time to maximum gape. Further, it appears cyprinodontiforms can alter the contribution of the premaxilla to mouth closure on an event-specific basis. We were able to demonstrate that, within at least one species, this variability is associated with the location of the prey (bottom vs. water column). Cyprinodontiform upper jaw movements likely reflect increased dexterity associated with a foraging ecology where prey items are "picked" from a variety of locations: the bottom, water column, or surface. We postulate that dexterity requires slow, precisely controlled jaw movements; thus, may be traded off for some aspects of suction-feeding performance, such as protrusion distance and speed.

***Keywords:*** Feeding kinematics; Teleost fishes; Atherinomorpha; Percomorpha

## Introduction

In Cypriniformes (Ostariophysii) and Percomorpha, two of the largest and most successful groups of teleost fishes, a mobile, bony element of the upper jaw (formed by the paired premaxilla bones) projects toward the prey item during feeding. Although jaw protrusion has evolved independently in each of these two groups, the protrusible premaxilla of both groups has a similar shape, with an ascending process (dorsal to the neurocranium), a rostral surface, and a descending process that projects ventrally, toward the lower jaw

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(Alexander, 1967a, 1969; Fig. 1). In representatives of both the general percomorph and cypriniform lineages, the movements of the upper jaw during feeding are similar: the premaxilla rotates dorsally and is simultaneously projected ventrally (Fig. 1A). Anterior movement of the paired descending processes serves to occlude the "V" created by the open mouth, which may prevent prey from escaping through the sides of the mouth (Motta, 1984). In addition, the anterior movement of the paired descending processes helps to form a tubular mouth opening. This type of small, rounded gape is associated with increased suction production during prey capture (Norton and Brainerd, 1993; Wainwright et al., 2001; Wainwright and Day, 2007).

However, one large and successful group of teleosts, the Cyprinodontiformes (Atherinomorpha), demonstrates a notably different upper jaw protrusion mechanism. In this group, the descending process of the premaxilla is bound by taut ligaments to the posterior lower jaw (mandible). Because of this attachment, the descending process cannot swing anteriorly during mouth opening and does not laterally occlude the open mouth (Fig. 1B). The dorsal elements of the premaxillae consequently protrude in a ventral direction, creating a characteristic beak-like appearance during prey capture (Alexander, 1967a; Fig. 2). A lip membrane is pulled taut during protrusion and in some taxa this membrane serves to partially occlude the sides of the open mouth (Fig. 2). Therefore, cyprinodontiform upper jaw protrusion appears to be generally different in both underlying morphology and mechanics of movement, relative to the cypriniform and generalized percomorph mechanisms.

Ecologically, the Cyprinodontiformes are largely "pickers" – predators that procure individual prey items from the water column, surface, or bottom (Weisberg, 1986; Mansfield and McArdle, 1998; Taylor, 1992; Hargrave, 2006). This trophic habit is likely related to the distinctive feeding mechanism found within this clade, leading us to pose the general question: is there a performance trade-off associated with beak-like, cyprinodontiform premaxillary protrusion? Theoretically, jaw protrusion confers a number of advantages during prey capture, including: increasing both stealth and prey capture velocity by allowing the fish to protrude a small element rapidly towards the prey item (as opposed to

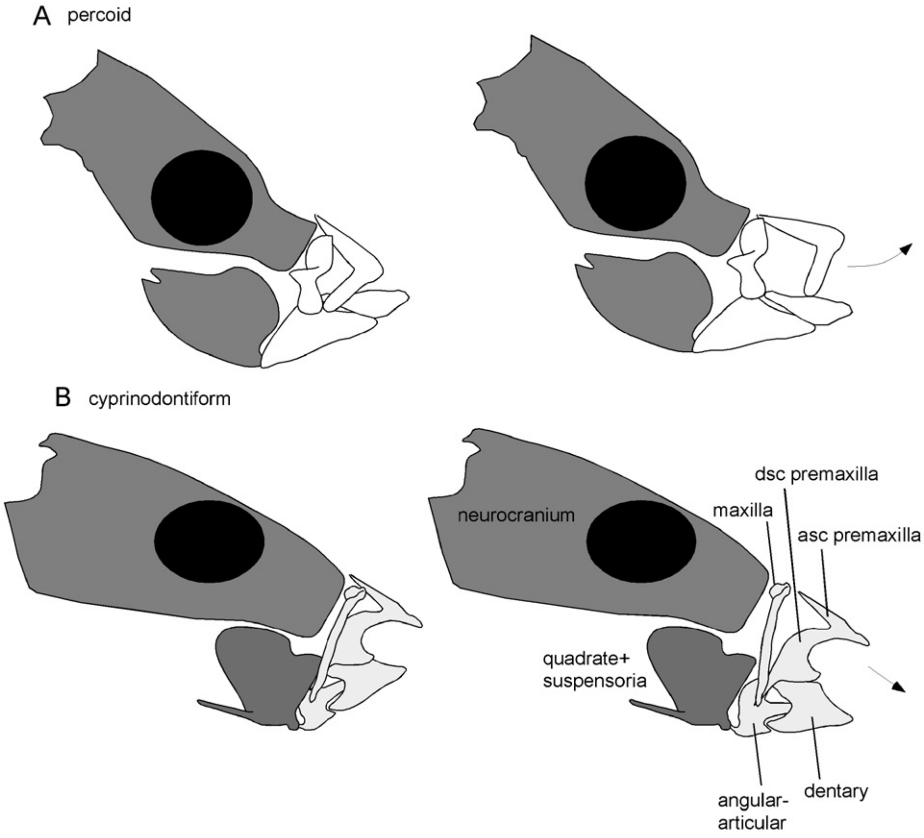

**Fig. 1.** Skeletal anatomy of a generalized percoid (A) and cyprinodontiform (B). Superficial bones have been removed, the neurocranial and suspensorial details are highly reduced to make the upper and lower jaw elements more apparent. Key elements are labeled, abbreviations as follows: asc, ascending process; dsc, descending process. The general direction of motion of the protruding premaxilla is indicated by arrows. Note the position of the descending process of the premaxilla, which is bound tightly to the dentary by ligamentous connections.

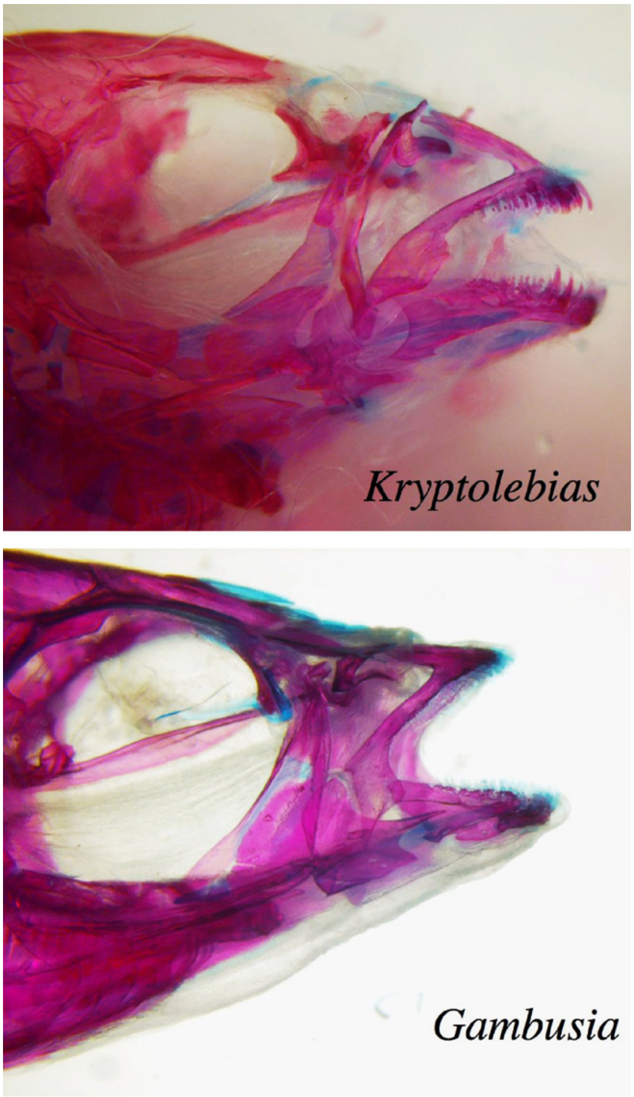

**Fig. 2.** Cleared and stained images of two cyprinodontiform taxa showing the consistency in premaxilla shape, the beak-like premaxillary protrusion, and the presence of the lip membrane in *Kryptolebias*.

accelerating the entire body; Motta, 1984; Waltzek and Wainwright, 2003); increasing water velocity, and therefore suction production, during feeding (Schaeffer and Rosen, 1961; Motta, 1984; Norton and Brainerd, 1993); and enabling a fish to close its mouth rapidly by decreasing the distance between the upper and the lower jaws (Alexander, 1967a). It is not known if the cyprinodontiform premaxillary protrusion mechanism facilitates these particular aspects of prey capture performance, or if it enhances some other aspect of performance. Although the enhancements to feeding performance listed above may still provide a performance advantage for this group, it is also possible the unusual morphology and feeding habits of the cyprinodontiforms have placed a demand on the feeding apparatus that has resulted in a functional trade-off in other aspects of feeding performance.

Thus, we hypothesize that the beak-like morphology of the cyprinodontiforms enhances certain aspects of feeding performance, but that this enhancement comes at a cost to other aspects of feeding performance. To test this hypothesis, we measure the movements of the premaxilla during feeding in four cyprinodontiform species, chosen to represent different phylogenetic positions within this large and successful teleost order. We compare these data within and among the selected cyprinodontiform taxa to determine the variation in upper jaw movements inherent within the group. We also compare these data with those from three general percomorph species in order to place this variation within a comparative context. Using these kinematic comparisons, we address the following specific questions about potential functional trade-offs. Does the type of upper jaw protrusion mechanism affect (1) the degree to which the jaws can be protruded, (2) the ultimate size or shape of the mouth opening during prey capture, (3) the speed of the prey capture event, or (4) the ability to close the jaws rapidly during the prey capture event? Or, does upper jaw protrusion enhance some other, previously unidentified, aspect of feeding performance within the Cyprinodontiformes?

## Methods

Four cyprinodontiform species were selected for study (Fig. 3): *Poecilia sphenops* (Poeciliidae; size range 4.8–5.2 cm total length (TL)), *Gambusia affinis* (Poeciliidae; size range 2.4–3.9 cm TL), *Fundulus rubrifrons* (Fundulidae; size range 3.7–4.4 cm TL), and *Kryptolebias marmoratus* (Rivulidae; size range 3.2–3.8 cm TL). These taxa were selected because they represent a range of morphological conditions in terms of the presence of the lip membrane, which occludes the sides of the open mouth (to create a more or less rounded mouth aperture) and determines the degree of beak-like protrusion exhibited in manipulations of cleared and stained specimens (see Fig. 2). In addition, for *G. affinis*, we had two prey-location treatments: midwater and benthic. This allowed us to quantify the potential kinematic variation in upper jaw movements within one species in an experimentally controlled manner.

To compare different types of protrusion mechanisms (cyprinodontiform vs. percomorph), we used datasets for three distantly related percomorph taxa. These species were selected because they also forage on small, mobile midwater invertebrate prey, and are of approximately the same head size as the cyprinodontiforms used in this study. Percomorphs used were female *Betta splendens* (Osphronemidae, Perciformes; size range

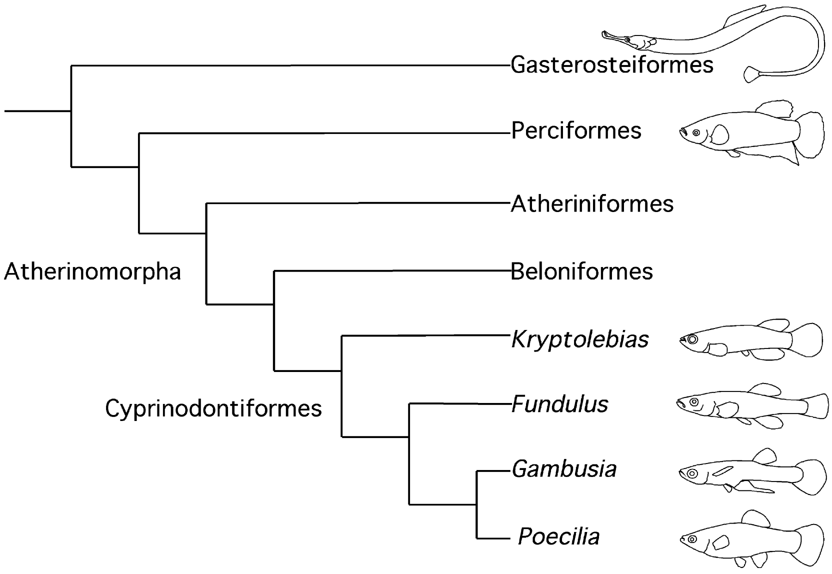

**Fig. 3.** Hypothesized percomorph relationships relative to the species of study. Traditional phylogenies place the Atherinomorpha as a derivative of the mullets and their relatives (sensu Eaton, 1935; Nelson, 2006), often outside the Percomorpha. Such placement strongly influences the type of jaw protrusion likely to be found in any hypothetical ancestor to the atherinomorphs. Recent molecular phylogenies, however, consistently place the atherinomorphs as a crown group among acanthopterygians (Miya et al., 2003; Mabuchi et al., 2007), as we have presented here. Relationships within Cyprinodontiformes are after Nelson (2006) and following Parenti (2005). Drawings are included for each representative group studied. Line drawings of each group are original drawings or after Nelson (2006).

4.0–5.2 cm TL), pipefish *Syngnathus leptorhynchus* (Syngnathidae, Gasterosteiformes; size range 22.4–26.7 cm TL; but note that the heads were comparable to the species studied here despite their elongate bodies), and the butterflyfish *Chaetodon xanthurus* (Chaetodontidae, Perciformes; size range 6.0–6.6 cm TL). While bettas and pipefish have aspects of their morphology that are modified for specific functions, we note that female bettas lack specializations to the jaws for fighting (unlike male bettas), and that pipefish jaws function in a manner similar to most perciform jaws, despite highly elongate cranial elements (Bergert and Wainwright, 1997). We selected *Chaetodon* specifically because it possesses one of the few examples of beak-like protrusion within the broader Percomorpha. Details regarding data collection for these three species have been published elsewhere (Ferry-Graham et al., 2001; Gibb and Ferry-Graham, 2005; van Wassenbergh et al., 2007), but the methods are consistent with those for the cyprinodontiforms, as described below. A number of additional variables were measured from the original footage for the purposes of the comparisons made here.

For kinematic analysis, at least four individuals of each species were filmed capturing either live or thawed adult *Artemia*, or thawed *Chironomus* larvae using a Redlake PCI 1000S MotionScope digital-imaging system recording at 250–500 frames per second. For feeding trials, individuals were placed in small (~15 cm × 15 cm × 20 cm) chambers. In some instances, two individuals easily distinguished by their relative size, sex or coloration were placed in one section. During feeding trials, all individuals were imaged from a lateral aspect; the feeding arena was illuminated by two 500 W tungsten photo-lamps and a ruler was recorded in the field of view for scale. Feeding events were initiated by introducing food a few pieces at a time into the feeding arena via pipette. Multiple capture events were recorded during a given feeding trial until the individual was satiated (i.e., the fish showed no interest in eating additional food items when presented). Individuals were maintained in the feeding arenas over a period of days until the necessary prey capture sequences were collected, and at least four sequences were obtained from each individual.

Four prey capture sequences per individual were digitized using NIH Image-J (Mac OSX, v 1.37) to quantify movement of pertinent cranial elements during the prey capture event. Images were only analyzed if the individual remained perpendicular to the camera throughout the capture event. Time zero ($t_0$) was defined by the onset of mouth opening. To assess upper jaw movements and their relation to jaw closure, we tracked four points in the anterior head and jaws over the course of the entire prey capture sequence (Fig. 4): (1) the anterior tip of the lower jaw, (2) the articulation between the lower jaw and the suspensorium (at the quadrate bone), (3) the anterior tip of the premaxilla, and (4) the anterior end of the nasal bone. These points were used to calculate two linear displacement variables in the fish frame of reference: gape (point 1 to point 3), and upper

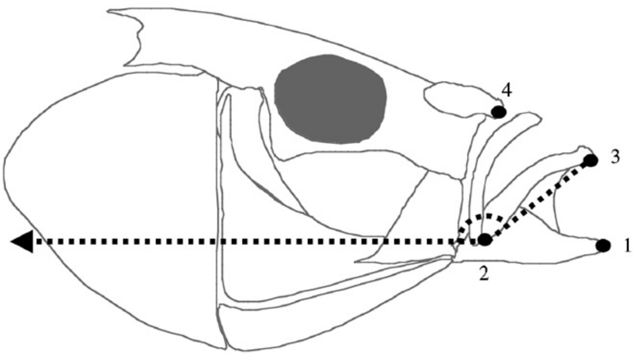

**Fig. 4.** Schematic illustration depicting the underlying skeletal elements that were digitized from the high-speed video footage. Numbers 1–4 are landmarks used for calculating displacements (see text). The dashed line illustrates how the angle of the descending process of the premaxilla was measured relative to the long axis of the body.

jaw protrusion (the straight-line distance between point 4 at $t_0$ and point 3 at any time $t$). The angle of the premaxilla with respect to the mid-coronal plane of the body was measured directly from the images using Image-J at three discrete points in time (Fig. 4): time zero ($t_0$), peak gape, and mouth closure. Moreover, for *Gambusia* benthic and midwater feedings we also measured the angle of the midline of the body relative to a horizontal line, as determined by the base of the tank, at time zero. The time to maximum gape and time to maximum upper jaw protrusion were also calculated for each prey capture event.

The displacement and timing variables were compared among all species using MANOVA (SPSS 11 for Mac OSX), with species as a single fixed effect. We employed a conservative approach and used means of each variable for each individual; thus, our sample size for each test was $n = 4$, which reflects the true level of replication. As the MANOVA indicated significant differences existed, ANOVA was performed as a post hoc test to determine which variables demonstrated differences among species. The $F$-values were significant in all cases, so Fisher's PLSD post hoc tests were used to determine which species were different from one another. For the within-species comparisons of *Gambusia*, jaw and body variables were compared among prey treatments (midwater and benthic) using two-sample $t$-tests (SPSS 11 for Mac OSX).

## Results

In all cyprinodontiforms, midwater prey were taken using a characteristic "nipping" motion, where only the tips of the premaxilla (upper jaw) and dentary (lower jaw) came into contact during the initial stages of mouth closing (Fig. 5). This was true regardless of the degree to which the lip membrane was present and/or extended anteriorly during prey capture. Among the other percomorphs studied, *Chaetodon* was the most similar to the cyprinodontiform fishes in that the upper and lower jaws also were used in what appeared to be a biting behavior. *Betta* and *Syngnathus* displayed the more typical percomorph pattern of a small mouth opening, which was laterally occluded by the descending process of the premaxilla. Prey were rarely captured between the jaws in these two species, as they were drawn fully into the buccal cavity, presumably by suction.

The taxa studied differed in the absolute displacement of the premaxilla during capture of comparable midwater food items (MANOVA Wilk's $\Lambda = 0.003$, $p < 0.0001$; Figs. 6 and 7), both in terms of the maximum anteriorly directed premaxillary protrusion achieved (ANOVA $F = 74.34$, $p < 0.0001$) and the resultant maximum gape distance achieved ($F = 12.75$, $p < 0.0001$). Post hoc tests revealed that within cyprinodontiforms, *Poecilia* had the largest maximum gape, exceeding 0.2 cm, followed by *Kryptolebias* and *Fundulus* at about 0.15 cm each, and then by *Gambusia* which averaged about 0.1 cm maximum gape (all $p < 0.003$, Fig. 6). The percomorph *Betta* had the largest maximum gape among all taxa studied, averaging nearly 0.6 cm (all $p < 0.04$, Fig. 7). *Syngnathus* and *Chaetodon* were not significantly different from *Kryptolebias*, *Fundulus*, and *Gambusia* (all $p < 0.02$, Fig. 7). Within cyprinodontiforms, maximum premaxillary protrusion was larger in *Poecilia* and *Fundulus* than in *Gambusia* and *Kryptolebias*; ~0.1 cm vs. ~0.05 cm in the latter (all $p < 0.008$, Fig. 6). Maximum premaxillary protrusion was greater in all three percomorph taxa, ranging from approximately 0.15 to 0.2 cm, than in any of the cyprinodontiform taxa (all $p < 0.001$, Fig. 7). Differences in absolute gape distance may incorporate minor body-size effects among the species studied. However, *Betta* was not the largest species studied, and it had the largest gape. Similarly, *Chaetodon* was among the largest in TL, and had one of the smallest gape distances. Premaxillary protrusion varied in a manner highly inconsistent with body size; thus, observed differences are not likely a simple consequence of animal size.

Species also differed with regard to the speed of the prey capture event, as assessed by time to reach peak gape, on comparable food items (ANOVA $F = 12.38$, $p < 0.0001$; Fig. 6): *Poecilia* and *Gambusia* both took about 0.04–0.05 s to reach peak gape, which was slower than *Fundulus* and *Kryptolebias* who took only 0.02–0.03 s (all $p < 0.005$). All three percomorphs achieved peak gape faster than the cyprinodontiforms; peak gape was achieved in ~0.005 s in *Syngnathus*, ~0.01 s in *Betta*, and 0.02 s in *Chaetodon*. However, there was enough variation in this timing that the differences between the percomorphs and *Fundulus* and

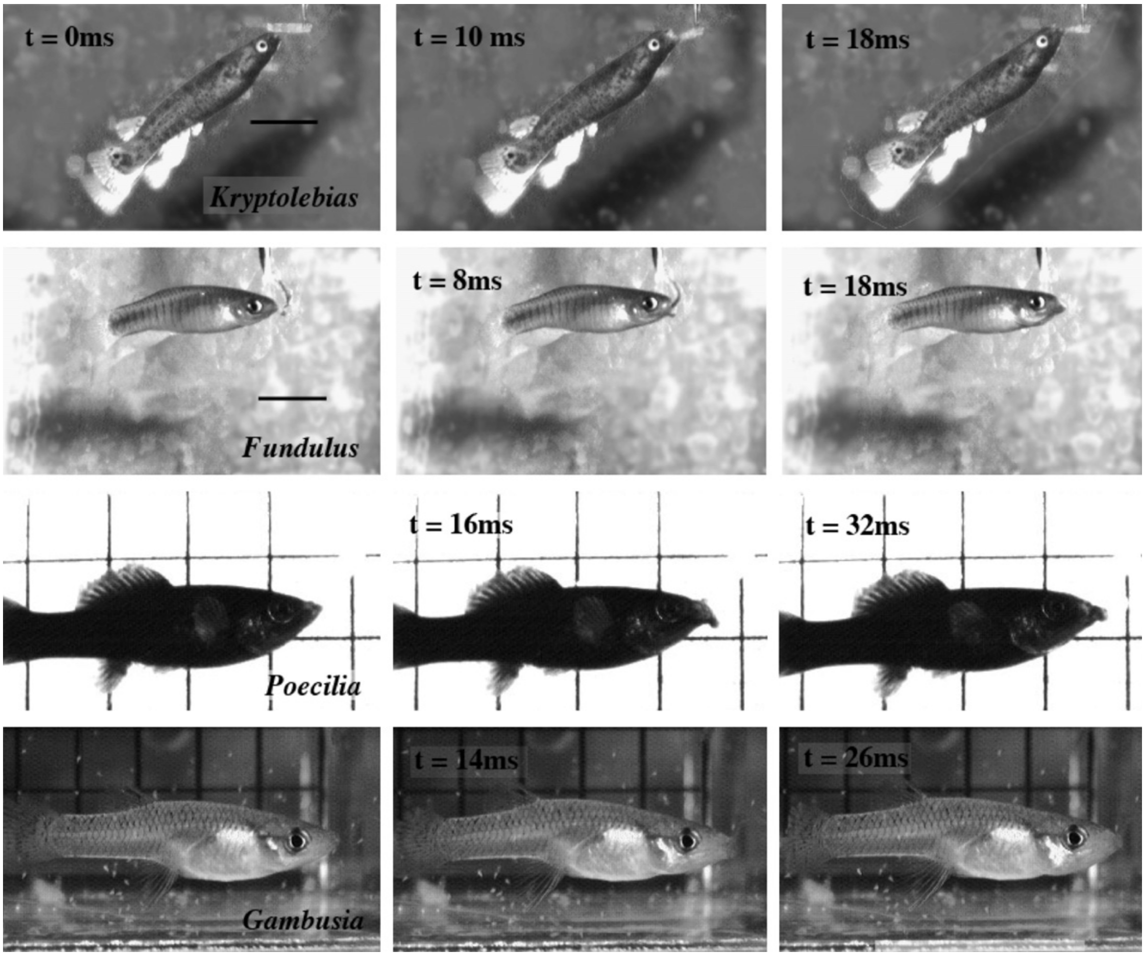

**Fig. 5.** Composite video image featuring midwater prey capture events by *Kryptolebias marmoratus*, *Fundulus rubrifrons*, *Poecilia sphenops* and *Gambusia affinis.* Depicted from left to right: time zero, or the time of mouth opening, peak gape, and mouth closure (time increments indicated on sequences). Scale bars are 1 cm; grids are 1 cm × 1 cm.

*Kryptolebias* were not significant. This is also not an effect of size, as *Gambusia* was among the smallest animals included in the study and thus would be expected to be among the fastest feeders.

The degree to which the premaxilla was protruded at the time of mouth closure during midwater captures also varied among species. On average, premaxillary protrusion made the greatest contribution to mouth closure in *Fundulus* (Figs. 6 and 7). In this species, premaxillary protrusion distance was greatest at the time of complete mouth closure, at slightly over 0.1 cm. As in all cyprinodontiforms studied during the capture of midwater prey, the angle of the premaxilla was greater at peak gape than at $t_0$, meaning it rotated ventrally and assumed a more horizontal position relative to the mid-coronal plane of the body (Fig. 8). This angle was still greater at mouth closure, rotating by ~6° at the time of peak gape and ~20° by the time of mouth closure (Fig. 8).

In *Kryptolebias*, premaxillary protrusion also contributed to mouth closure – maximum premaxillary protrusion was achieved as the mouth was closing (i.e. during lower jaw elevation), although prior to complete closure (Fig. 6). The angle of the descending arm of the premaxilla relative to the body increased by only about 5° at the time of peak gape (Fig. 8). In this species, a very large amount of cranial rotation appeared to contribute to mouth opening (LFG, pers. obs.). During mouth closing, the premaxilla angle increased another 10° relative to its position at peak gape (Fig. 8).

Interestingly, in *Poecilia*, the premaxilla reached its maximum excursion when the mouth was approximately half closed; during this time period, the gape is being reduced at the fastest rate, as is demonstrated by the slopes of the lines for gape distance (Fig. 6). This mouth-closing pattern was consistently the most similar to the percomorphs included for comparison (Fig. 7). The angle of the premaxilla increased greatly during the strike relative to its position at $t_0$, by about 10° at peak gape, and over 40° at the time of mouth closing (Fig. 8).

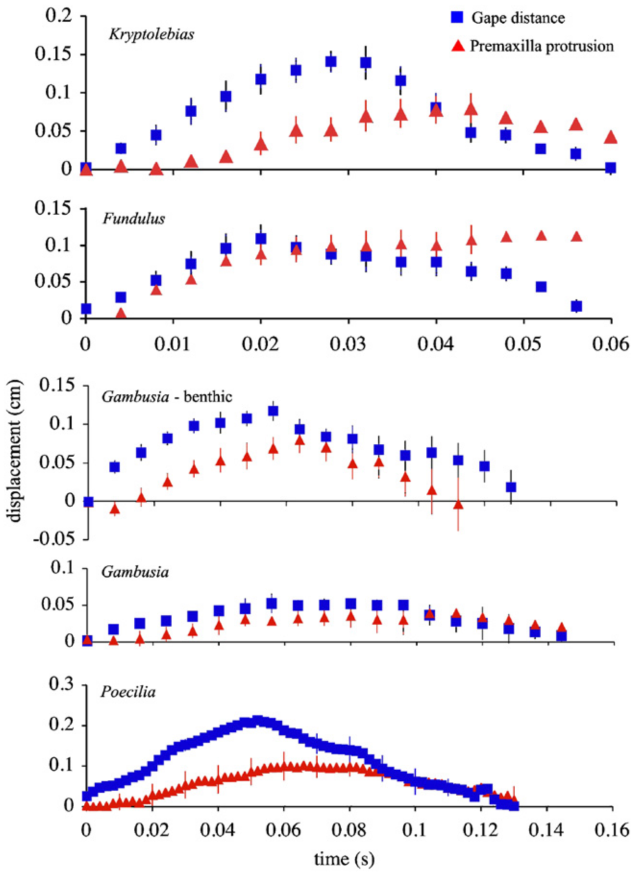

**Fig. 6.** Kinematic profiles of premaxillary protrusion and gape distance as determined from high-speed video in cyprinodontiform taxa. Profiles illustrate kinematics of *Kryptolebias marmoratus*, *Fundulus rubrifrons*, *Gambusia affinis* and *Poecilia sphenops*. All profiles are for midwater feedings except for *Gambusia affinis* where noted. Note that the time, or *x*-axis, scale is different for various panels. Gape distance is indicated by boxes and premaxillary protrusion distance by triangles. Values shown are means from all strikes for each species; error bars are ±one standard error of the mean.

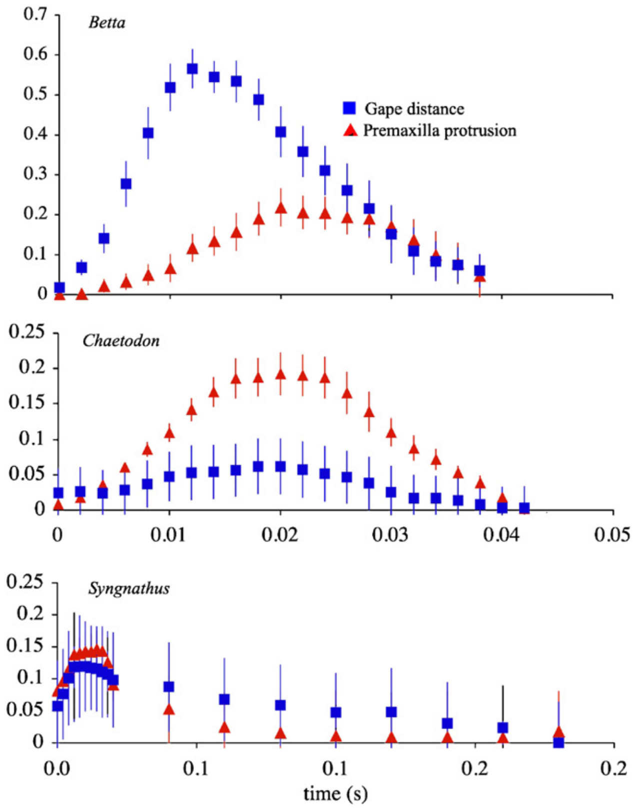

**Fig. 7.** Kinematic profiles of premaxillary protrusion and gape distance as determined from high-speed video in acanthopterygian taxa. Profiles illustrate kinematics of *Betta splendens*, *Chaetodon xanthurus*, and *Syngnathus leptorhynchus* capturing midwater prey. Note that the time, or *x*-axis, scale is different for various panels. Gape distance is indicated by boxes and premaxillary protrusion distance by triangles. Values shown are means from all strikes for each species; error bars are ±one standard error of the mean.

*Poecilia* achieved the most extreme angle of the premaxilla relative to the body among the taxa studied here, occasionally exceeding 180°.

Midwater prey capture events by *Gambusia* were much like those of *Fundulus* in terms of the angle of the descending process of the premaxilla during prey capture, though with less rotational movement occurring between time zero and mouth closure (Fig. 6). During midwater feeding events the angle of the premaxilla increased by about 7° at the time of peak gape and by only another 3° at the time of mouth closure (Fig. 8).

The position of the prey in the water column affected premaxillary kinematics and the contribution of the premaxilla to mouth closing. Benthic prey capture events were comparable to midwater events in terms of the time to reach peak gape: in both it took about ~0.05 s (Fig. 6); however, the premaxilla completed its excursion about ~0.04 s faster in benthic events. Maximum premaxillary protrusion more than doubled in benthic feedings relative to midwater feedings (0.05 vs. 0.12 cm, $t = 5.185$; $p < 0.0001$). This may be related to body angle, as substrate-feeding *Gambusia* held their bodies at significantly greater angles with respect to the bottom relative to midwater-feeding *Gambusia* (benthic food items were taken with the body oriented towards the bottom at an angle of $-32.93 \pm 1.93°$ vs. a slight upward orientation of $4.92 \pm 5.24°$ for midwater food items; $t = 19.61$, $p < 0.0001$). Despite the large degree of premaxillary protrusion during benthic feeding events, the premaxilla typically returned to its resting position against the maxilla before the gape distance was reduced to zero; this means the premaxilla did *not* contribute to jaw closure and that the premaxilla appeared to move caudally independent of the movements of the lower jaw. Thus, the distance between the jaw tips was reduced primarily via a rapid movement of the lower jaw

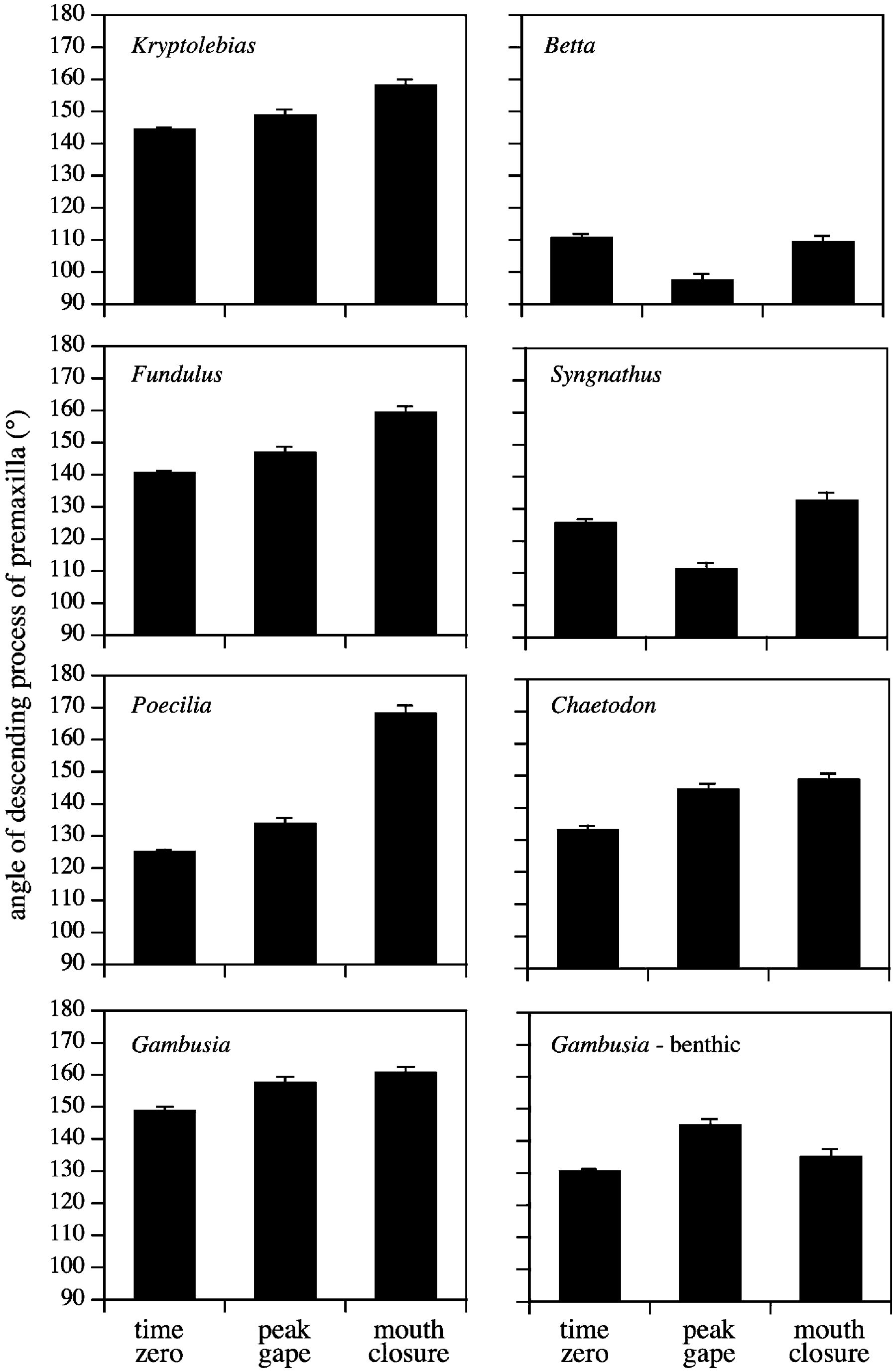

**Fig. 8.** Graph illustrating the angle of the descending process of the premaxilla relative to the mid-coronal plane of the body. Profiles illustrate premaxilla movements for the cyrpinodontiforms *Kryptolebias marmoratus*, *Fundulus rubrifrons*, *Poecilia sphenops*, and *Gambusia affinis* (benthic and midwater), and the acanthopterygians *Betta splendens*, *Syngnathus leptorhynchus* and *Chaetodon xanthurus*, as indicated. Increasing values indicate that the premaxilla is moving ventrally, or is more horizontally oriented; 180° would be parallel with the mid-coronal plane of the fish's body. Values shown are means from all strikes for each species; error bars are ±one standard error of the mean. Times at which angles were measured were time zero, or the time of mouth opening, time of peak gape, and time of mouth closure.

towards the upper jaw during benthic events (Fig. 6). The angle of the premaxilla increased at peak gape, relative to $t_0$, by a little over 10°, but the angle at mouth closure had returned to an angle nearly identical to the starting angle (Fig. 8).

Of the percomorphs selected for comparison, only *Chaetodon* showed the basic cyprinodontiform-like pattern of a steady increase in premaxillary angle throughout the strike (Fig. 8). *Betta* and *Syngnathus* achieved much smaller angles, and the value was closer to 90° at peak gape, which tended to be the minimum angle recorded among the times examined (Fig. 8).

## Discussion

Most teleosts rely on ram or suction, or some combination of the two (Norton and Brainerd, 1993), to capture prey. The ability to produce suction effectively has been linked explicitly to the ability to protrude the premaxilla, and a number of purported performance advantages are conferred by that ability. These advantages include: increasing stealth and prey capture velocity (Waltzek and Wainwright, 2003); increasing water velocity, and therefore suction production (Schaeffer and Rosen, 1961; Motta, 1984; Norton and Brainerd, 1993); and enabling a fish to close its mouth rapidly (Alexander, 1967a).

The stealth of the attack has been linked functionally to the amount of anteriorly directed protrusion of the premaxilla (Waltzek and Wainwright, 2003). Based on our outgroup comparisons, it appears that the cyprinodontiform upper jaw protrusion mechanism may restrict anteriorly directed premaxilla protrusion. Maximum anteriorly-directed premaxillary protrusion was always larger in the percomorphs studied than in the cyprinodontiforms. Thus, when compared to the three percomorphs, there appears to be a limit to which the beak-like upper jaw of the cyprinodontiform taxa can be projected. Given this limitation, the stealth of the cyprinodontiform attack is likely reduced relative to the more rapid percomorph attack.

Higher velocity events should result in higher velocities of water drawn into the mouth, and concomitant higher suction production (Schaeffer and Rosen, 1961). Consistent with the above observations regarding the lip membrane, *Fundulus* and *Kryptolebias* had faster prey capture events than *Poecilia* and *Gambusia*, further suggesting the possibility of enhanced suction production ability within these two cyprinodontiform taxa, relative to the others examined here. However, relative to the three percomorphs studied, all cyprinodontiforms took longer to reach peak gape. Thus, it appears that the cyprinodontiforms' mechanism may incur a performance cost in at least one aspect of suction production ability, as a reduction in feeding velocity likely reduces the suction generated by the buccal cavity during the strike. This functional trade-off, however, does not appear to result in a complete failure of suction production during the strike as some movement of the prey towards the predator was noted in 100% of *Gambusia* and *Poecilia* midwater feedings (LFG, pers. obs.).

Higher water velocities for generating suction are functionally linked with the ability to create a small, rounded mouth opening (Norton and Brainerd, 1993; Alexander, 1967a). The mouth opening, as assessed by gape distance, is not systematically different in the cyprinodontiforms relative to the percomorphs examined here. However, as noted from the onset, cyprinodontiforms lack the general percomorph ability to create a small, rounded mouth opening via the descending processes of the maxilla. For this reason, *Kryptolebias* and *Fundulus* were selected for study, as they both possess a discrete lip membrane that connects the upper and lower jaws. Gosline (1981) proposed that this membrane was responsible for jaw protrusion, but this has since been disproven (Hernandez et al., 2008). However, the lip ligament certainly occludes the sides of the open mouth in some cyprinodontiform species, and thus could serve to enhance suction ability. *Fundulus* and *Kryptolebias* exhibited the fastest prey capture events among cyprinodontiforms, consistent with the potential for increased suction production ability in these two species.

Increased absolute premaxillary protrusion can also lead to increased suction production and has been putatively tied to increased prey capture success (Motta, 1984). However, benthic feedings by *Gambusia* employed a larger amount of upper jaw protrusion relative to midwater strikes, and *Gambusia* often missed the prey item in this setting. Benthic feedings were unsuccessful 25% of the time; midwater feedings were unsuccessful 0% of the time in *Gambusia*, and in all other species studied here. In the successful benthic captures, suction appeared to contribute to prey capture approximately one-third of the time. In these sequences, the prey item was drawn directly into the buccal cavity without coming into contact with the tips of the upper and lower jaws. In the remaining two-thirds of the benthic feeding events, the prey items were captured by initially being grasped between the tips of the upper and lower jaws. This is in contrast to the consistent contribution of suction during midwater strikes, as noted above. These results seem to suggest that there was less effective suction production, and less prey capture success, during benthic feeding events despite the increased jaw protrusion. This runs counter to the recent finding that feeding near the substrate makes suction more effective by extending the distance over which an effect can be produced (Nauwelaerts et al., 2007). In a picking prey capture context, increased premaxillary protrusion may instead lead to increased rapidity of the bite, which may be essential when the body is held at extreme angles relative to the substrate and vigilance is temporarily prevented thereby increasing predation risk during the feeding event (Motta, 1984). Indeed, benthic prey capture is faster than midwater prey capture for *Gambusia*, at least in terms of complete cycle time for both gape and premaxilla protrusion (Fig. 6).

The benthic feedings examined here for *Gambusia* also deviated from the general teleostean pattern of premaxillary protrusion contributing to mouth closure. In percomorph and cypriniform teleosts, the protrusion of the premaxilla is generally regarded as essential to mouth closure, because the rapidly protruding premaxilla meets the ascending lower jaw and enables the jaws to make contact more quickly (Alexander, 1967b). Indeed, we observed that while highly variable, the premaxilla tended to contribute to jaw closing to some degree in all taxa studied. It contributed the most in *Fundulus* and *Kryptolebias*, the cyprinodontiforms with the fastest prey capture events and the most rounded mouth openings, but less in other cyprinodontiform taxa with slower capture events and more beak-shaped mouth openings. The relative reduction in the contribution of the premaxilla to mouth closing in these species is somewhat surprising because the direction of protrusion in Cyprinodontiformes should, at least theoretically, make contact between the upper and lower jaws during mouth closure that much easier to achieve. Thus, one might predict that all cyprinodontiforms should have a greater contribution of premaxillary protrusion to mouth closure relative to percomorphs. Instead, in several cyprinodontiform taxa, the premaxilla reached its maximum displacement and reversed direction before coming into contact with the lower jaw. This pattern was most prominent in substrate-feeding *Gambusia*.

The ability of *Gambusia* to modulate the movements of the premaxilla in response to specific feeding situations, however, speaks to the ability of cyprinodontiforms to exert fine control over the feeding mechanism and its deployment. The ballistic movements produced by the head and jaws during suction-based prey capture are explosive in nature, and likely allow little time for on-line correction of movement (Deban et al., 2001). In contrast, more precise control of the jaws is likely required when using a picking mode of prey capture. In a picking-based feeding mode, the jaw tips are used for grasping individual prey from the water column or benthos. The ability to place the anterior tips of the upper and lower jaws on a specific, small prey item requires dexterity in jaw movements. That *Gambusia*, for example, can modulate the movements of the premaxilla in response to specific demands of the feeding event implies that they have exceptional control over the jaws during the feeding event. While the ability to modulate premaxillary movements was not investigated for other taxa within this study, it has been previously reported for species of *Fundulus* (Alexander, 1967a). This suggests that such dexterity, at least in terms of movements of the premaxilla, may be prominent within the clade as a whole.

We argue that increased dexterity incurs a functional trade-off: decreased strike velocity. Indeed, as noted previously, the time to peak gape tended to be greater in the cyprinodontiforms relative to the percomorphs in this analysis. Similarly, both the time to peak gape and the total strike duration tended to be greater in *Gambusia* (midwater and benthic) and *Poecilia* relative to *Kryptolebias* and *Fundulus*, suggesting that speed may be sacrificed in favor of enhanced dexterity in the more beak-like jaw protrusion of *Gambusia* and *Poecilia*. *Poecilia* had both the longest strike duration and the greatest premaxillary protrusion among cyprinodontiforms. These modifications are likely related to further increases in dexterity, as *Poecilia* are among a handful of cyprinodontiforms that have secondarily evolved a grazing habit (Zaret and Rand, 1971; Fares Alkahem et al., 2007) and grazers employ direct contact between the jaws and the substrate (in a biting or scraping motion) to obtain food items. In *Poecilia*, dexterous jaw movements facilitate maximum contact between the teeth of the jaws and the substrate (Gibb et al., in press).

The more general cyprinodontiform ability to select a specific item from the surrounding medium may enable fishes with a picking-based mechanism to avoid the complications of post-ingestion prey processing. Fishes with a suction or ram-based prey capture mechanism are often relegated to separating the nutritive portions of ingested prey from the non-nutritive via elaborate mechanisms associated with prey processing (Wainwright, 1989; Drucker and Jensen, 1991; Wainwright et al., 1991; Dean et al., 2005). With these structures (e.g., pharyngeal jaws and hydrostatic or muscular tongues), sorting can only be accomplished *after* the prey item and associated non-nutritive materials have been captured and brought into the mouth. Indeed, a putative reason for the evolution of these elaborate structures is to compensate for the lack of a refined, or specific, prey capture mechanism (Dean et al., 2005). We posit that cyprinodontiform fishes circumvent this problem by eliminating the ingestion of non-nutritive items entirely.

We note that the character state of having the premaxilla "pinned" to the maxilla, thus creating the beak-like protrusion characteristic of the cyprindontiforms, has evolved several times outside of this clade. For example, the stickleback *Gasterosteus aculeatus*, and presumably other members of the Gasterosteidae (although not their close relatives, the seahorses and pipefishes), have a long descending process of the premaxilla that is attached by a ligament to the maxilla at its distal end, and the two bones are connected to the mandible by a second ligament (Gregory, 1933). Indeed, Gregory (1933) described several aspects of the skull of gasterosteids as being of the "poeciliid type". In their description of the mojarras (Gerreidae), Schaeffer and Rosen (1961) similarly noted the attachment of the descending process of the premaxilla to the maxilla and lower jaw, and the anterior-ventrally directed protrusion of the premaxilla. Some of the chaetodontids, represented here by *C. xanthurus*, also possess this trait. Perhaps not surprising is that all of these species feed upon small invertebrates in the water column (Ferry-Graham et al., 2001; Ibraham and Huntingford, 1988; Campbell, 1991). However, despite its superficial similarity to the cyprinodontiforms, *Chaetodon* consistently exhibited kinematics (i.e., displacement and timing variables) more like other percomorphs than cyprinodontiforms. In addition, of these groups demonstrating beak-like protrusion of the premaxilla (i.e., gasterosteids, chaetodontids, gerreids, etc.), only the cyprinodontiforms appear to have undergone an extensive radiation, with the order containing over 1000 species (Nelson, 2006).

Historically, premaxillary protrusion has been credited with a number of performance advantages leading to improved prey capture success. The majority of these hypothesized performance advantages relate to enhanced stealth of feeding and/or suction production. However, the picking-based prey capture mode of the Cyprinodontiformes suggests a novel role for jaw protrusion within teleost fishes. In this group, premaxillary protrusion appears to allow fish to select individual prey items out of the water column or from the bottom, enhancing prey selectivity. We propose that this unusual mechanism of jaw protrusion enables the large and successful order Cyprinodontiformes to demonstrate diversity along an evolutionary axis quite different from the typical ram-suction continuum described for most midwater-feeding teleost fishes.

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